

Evolution of iterated Hawk-Dove games with quitting:  
Adaptive dynamics approach with population  
embedding

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<p>The Hawk-Dove game has been used as a model of situations of conflict in diverse fields as sociology, politics, economics as well as animal behavior. The iterated Hawk-Dove game has several rounds with payoff in each round.</p> <p>The thesis is about a version of the iterated Hawk-Dove game with the additional new feature that each player can unilaterally decide when to quit playing. After quitting, both players return to the pool of temporally inactive players. New games can be initiated by random pairing of individuals from within the pool.</p> <p>The decision of quitting is based on a rule that takes into account the actions of oneself or one's opponent, or on the payoffs received during the last or previous rounds of the present game. In this thesis, the quitting rule is that a player quits if its opponent acts as a Hawk.</p> <p>The additional feature of quitting dramatically changes the game dynamics of the traditional iterated Hawk-Dove game. The aim of the thesis is to study these changes. To that end we use elements of dynamical systems theory as well as game theory and adaptive dynamics.</p> <p>Game theory and adaptive dynamics are briefly introduced as background information for the model I present, providing all the essential tools to analyze it. Game theory provides an understanding of the role of payoffs and the notion of the evolutionarily stable strategies, as well as the mechanics of iterated games. Adaptive dynamics provides the tools to analyze the behavior of the mutant strategy, and under what conditions it can invade the resident population. It focuses on the evolutionary success of the mutant in the environment set by the current resident.</p> <p>In the standard iterated Hawk-Dove game, always play Dove (all-Dove) is a losing strategy. The main result of my model is that strategies such as all-Dove and mixed strategy profiles that are also not considered as worthwhile strategies in the standard iterated Hawk-Dove game can be worthwhile when quitting and the pool are part of the dynamics. Depending on the relations between the payoffs, these strategies can be victorious.</p>			
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# Chapter 1

## Introduction

The role of quitting, in nature as well as in games, exist as a strategic decision. Whether to retreat from threatening combat or avoid unfavorable situations, where the likelihood of winning is small, quitting is the rational decision to preserve resources. Suppose a predator chases after prey, but catching seems to be more distant by every second the chase continues. Here, it is favorable to quit the chase to preserve energy, which in turn can be utilized when a slower prey appears.

The rules of the game define a space, be it a ring, a board, or a field. Within the space, the sum of every interaction between players defines the strategy. A game needs not only rules and strategies but also a point. Possible payoffs of any form are the reason for a game to exist. Consider a match of boxing: Boxers aim to win the match. It can be either by knock-out or by gaining more points than the opponent. The essence here is to win, but the strategies to achieve this varies. From different outcomes, we can assume that quitting can occur in situations where the cost of leaving is lower than the cost of staying in the game. After quitting, the player goes to the pool of temporally inactive players, which resembles a waiting room for the players. From there, players are picked and paired to play against each other at the beginning of a new round. In such a game, under what conditions quitting is favorable behavior, and does it have any real-life applications?

As the saying goes: "A quitter never win, and winner never quits." The interesting question here is whether the initial setting is this simple? Previous research about quitting exists only barely in the field of game theory, a mathematical approach to games. Ollikainen (2018) discussed this phenomenon briefly in his thesis, leaving behind some open questions regarding quitting. An inclusive understanding of quitting is well analyzed in the field of psychology. For example, Fershtman and Gneezy (2011) studied quitting in tournament conditions, concluding that higher rewards may result in unintended outcomes in the form of higher dropout rates. Their experiment suggests that quitting increases in frequency as the rewards move up. Adding mathematical tools, more specifically a game theory and adaptive dynamics to analyze quitting, can result in a comprehensive understanding of mechanics and driving motives of quitting.

I approach the role of quitting by introducing the tools of both game theory and adaptive dynamics. Game theory provides the laws of the game, by which the players behave. The concept of pure- and mixed strategies, and the payoffs they produce are expressed in detail and with multiple examples. Based on the works of Nash (1951), the theory of optimal

strategies for individuals, which in turn establishes the stable equilibria, is introduced. Later, Nash extended his theory to consider not only one round game but also multiple round games, so-called iterated games. At the adaptive dynamics section, I seize on the works of Geritz *et al.* (1998), representing the concepts of invasion fitness, evolutionarily stable and convergence stable strategies. It sets up the mathematical framework for understanding the long-term evolution of strategies. Lastly, I discuss briefly the possibility of branching as an evolutionary event, where the monomorphic population branches into dimorphic population via disruptive selection.

The pinnacle of the thesis will be the model with quitting as a compulsory outcome of the game. The model I present is based on a typical iterated Hawk-Dove game with respect to a quitting rule. It states: A player quits and terminates the game if its opponent acts as a Hawk, they are then returned back to the pool as inactive players. Otherwise, if both act as a Dove, both players proceed to the ongoing rounds as active players. How it affects the dynamics of the game, and which strategies thrive in the environment set by the rule. Can a mutant strategy invade the resident population when quitting exists as a game rule? Do either of the pure-strategies have a chance in the game, or do we have to rely on the mixed-strategies? Using both the tools of the game theory as well as adaptive dynamics offers a great insight into the role of quitting in iterated games. To answer and back my claims, I present two lemmas with proofs, concerning the qualitative properties of the singular-strategies.

The structure of this thesis is the following: First, I present the tools in the form of game theory and adaptive dynamics. These two forms the fundamental base of the analysis that I use in the model. Then, I represent the iterated Hawk-Dove game model in detail and define two lemmas with proofs. The lemmas explain the behavior of the potential invasion event by the mutant-strategy. Lastly, in the discussion chapter, I go through this model's weaknesses and strengths. I talk about the possible expansion for it and what can be analyzed even further.

# Chapter 2

## Game theory

Game theory is a branch of mathematics devoted to the logic of decision making in different interactions, for example, social interactions, conflicts of interests, and market transactions. One of its initial aims was to find principles of rational behavior. In games involving at least two players, they are assumed to know all the information about the game and all the possible moves in it. Under these circumstances, rational behavior is assumed to be optimal against irrational behavior.

Players' decisions can change throughout the game, and the decisions made by the other players have an impact on other players. There must exist at least two choices for the players to act on, which are called strategies. The outcomes of those choices are dependent on the strategies of all other players. These outcomes must be in a well-defined preference order so that numerical payoffs, reflecting these preferences, can be assigned to all players and all outcomes.

In short, the game theory deals with social interactions by abstracting their formal and logical properties. Although real-life interactions and models are often too complicated even supercomputers to handle, for example, the neural network of the human brain, the simpler models can explain a great deal. I will present a few basic examples of game theory to back this latter claim.

**Example 2.0.1.** *Prisoner's Dilemma* describes a situation where two players are engaged in the game with two options to choose: *Cooperate* or *Defect*. Both players have been found guilty of possessing illegal drugs, and they are suspected of being dealers also. Both suspects are, by default, sentenced for one year in prison if they stay silent. These following options exist for both players: if both cooperate, in the form of staying silent, they each get one-year sentence in prison as a *Reward*. But if both players defect, in the form of betraying the other, they get sentenced for one extra year in prison as, a *Punishment*, for failing to join forces. If one player defects while the other cooperates, then the defector gets not sentenced at all as a *Temptation* while the cooperator is sentenced for the maximum time in prison: three years as a *Sucker's payoff*. The prisoners are not allowed to communicate and have no loyalty to each other, and therefore each must make their choices independently. The situation is represented in the following table, where the payoffs are for the row player.

	<i>Cooperate</i>	<i>Defect</i>
<i>Cooperate</i>	1 Year	3 Years
<i>Defect</i>	0 Years	2 Years

Table 2.1: Payoff matrix for Prisoner's dilemma

This raises a question: How will the rational player act in this case? By defecting, of course. No matter what the other player does, the payoffs favors defecting. Indeed, against a cooperating player, one gets away for free by defecting, whereas cooperation results in one year of sentence. Against a defecting player, one gets sentenced two years in prison by defecting but gets the maximum sentence of three years in prison by cooperating. Hence, *Defect* is always the best option, but here's the rub: the other player, being rational too, plays along the same lines. As a result, both players end up with two-year sentences in prison, which is one year more than cooperation would have produced.

This conclusion shows the dilemma here: it is always a better option to pick *Defect* than *Cooperate*, no matter what the other player chooses. The result here is sub-optimal for both players when the option for cooperating is valid but more unsafe in the fear of defection. Although, in experimental tests players more often prefer cooperation over defect (Guyer and Perkel 1972). Cooperation has a more positive image than defecting in our culture.

Prisoner's dilemma shows the value of cooperation but does not de facto explain cooperative behavior; it will be the result if this game is played multiple rounds because it minimizes the maximum years sentenced in prison. As long as players are only playing for one round, the Prisoner's dilemma is not, in fact, a dilemma at all. Defection is the only rational option to choose.

**Example 2.0.2.** *Hawk-Dove* (or 'Chicken') game gives a basic example of a contest between two individuals with different strengths and weaknesses for resource like food or territory. This model is also used to explain the evolution of aggression (Maynard Smith and Harper 1988). The strategies are Hawk (H) and Dove (D). Strategy Hawk will fight until it gets the resource or gets hurt, whereas Dove won't fight and either give up or shares the resource evenly if also the opponent plays dove.

	<i>Hawk</i>	<i>Dove</i>
<i>Hawk</i>	$\frac{1}{2}(R - C), \frac{1}{2}(R - C)$	$R, 0$
<i>Dove</i>	$0, R$	$\frac{1}{2}R, \frac{1}{2}R$

Table 2.2: Payoff matrix for a game of Hawk-Dove

In the table above, payoffs are explained for each possible outcome for the row player. The more aggressive behavior *Hawk* will escalate into a fight, with a cost C of fighting, until the injury decides the outcome. *Doves* will take a non-violent approach, and instead share the resource R than take the risk of injury in a fight. If most of the population are doves (specific description is: individuals playing strategy dove), the hawk strategy will spread like a wildfire, because doves will avoid fighting at any cost. But if most of the population are hawks, higher aggression within the population will lead the probability of injuring a

contestant to half. Depending on the severity of the injury, the contestant will rather avoid it and choose a peaceful approach, like a dove, in which both contestants get half of the resource.

In real-life, the rational player should avoid situations, where playing the simple game of Hawk-Dove is an only option, at any cost. An ordinary player cannot take every battle, it is too exhausting. You have to pick your battles wisely to withstand in the game. On the other hand, retreating from every conflict is sub-optimal. This situation calls for a better strategy, which is something between these two available, a mixed strategy to be more specific.

Hawk-Dove game has multiple variations where the payoffs are chosen to reflect the observed situations. For example, a display contest where the resource cannot be divided between the Dove players, and therefore the payoff is set to be zero for both players, instead of the regular version of the Hawk-Dove game showed above.

If we consider the possibility to play multiple rounds of Hawk-Dove game, different strategies can become unbeatable or perish depending of course on the set of mixed strategies that can be chosen by the players. Diverse conditions can spice up the dynamics of the game, for example, if the player plays at most 15 rounds of Hawk-Dove but only withstands a battle with another Hawk-player at most two times before retiring from the game. Often added conditions give a more realistic picture of real-world cases, where the payoff of one player depends on multiple choices of other players during an extended period, and navigating through all the possible options in the hope of finding the best possible outcome for oneself is hard.

To put these two examples into a mathematical framework, I will bring forward definitions and theorems which are required to move forward into a captivating examples and finally present my model.

Within a population, individuals can play any strategy from the strategies available for them. Depending on the game players are involved with, there might exist a finite amount of strategies available for them, like in a game of rock-paper-scissor. But all games are not equal in terms of their strategies available for the players. In a game of chess, there exists an almost infinite amount of possible choices for the players. The following definition is from the course notes but the ideas are presented in a book written by Weibull (1997, pp. 1-2).

**Definition 2.0.1.** A two-person game is defined in the following way:

1. Two strategy sets  $X$  and  $Y$ , are for each player, and the sets are well defined.
2. A payoff function  $\pi_i : X \times Y \rightarrow \mathbb{R}$ , where  $\pi_i$  is the payoff for  $i$ :th player.

As discussed briefly before, strategy sets can be from discrete up to infinite sizes, and they include all the possible strategies available for the players. But the strategies are linked up to payoffs in the following way: function  $\pi(x, y)$  gives the payoff for both players when one plays strategy  $x$  and the other plays strategy  $y$  from their respective strategy sets.

In the game with two alternative strategies available, there exist only three possible dynamics for two competing populations. One strategy may dominate over the other, fares better in every situation, no matter if it encounters another strategy or a copy of itself.

**Definition 2.0.2. (Dominant strategy solution)** A strategy  $x \in X$  is said to be dominated by  $x' \in X$  if  $\pi(x, y) \leq \pi(x', y)$  holds for all  $y \in Y$ . If the inequality is strict, we speak of



strong domination, otherwise of weak domination. The dominant strategy solution is a very good solution concept, because each player's best strategy is unaffected by the action of other player.

The other two dynamics are called bi-stable and coexistence. In a bi-stable game, each of the two alternative strategies is the best reply against itself, leading ultimately to one of the strategies to win. Whereas in the case of coexistence; each strategy is the best reply against the other strategy but not to itself. One strategy cannot overtake the other in population; this forces both populations to live side by side.

What if a player could outsource the decision-making process to probabilities that determine the pure strategy that the player will then play. A program based on a randomized decision is called a *mixed strategy*.

**Definition 2.0.3. (Mixed strategies)** Given a set of pure strategies  $x_1, x_2, \dots, x_k$ , we can represent mixed strategy by a vector of probabilities  $p_1, p_2, \dots, p_k$  where  $p_i \geq 0$  with all  $i$  and  $\sum p_i = 1$ . Here  $p_i$  is the probability to play strategy  $x_i$  in  $n$ -dimensional euclidean space  $\mathbb{R}^n$ . The set  $\{x_i : p_i > 0, i = 1, 2, \dots, k\}$  is called the support of the mixed strategy. This definition is readily generalized to countably many pure strategies or even a continuum of pure strategies.

One can consider pure strategy as a degraded version of a mixed strategy; one pure strategy is selected with probability one and every other strategy with probability zero. But mixed strategies have their shortcomings as they do not explain why and how players randomize their decisions.

From the groundbreaking notion of mixed strategies, we introduce the result of John Forbes Nash Jr. who invented a more general definition for the *equilibrium* in a game-theoretic concept. Nash (1951, Theorem 1) created a strategy profile, which is called a *Nash equilibrium*, if no player can do better, in a payoff wise, by unilaterally changing his or her strategy, then the current set of strategies and their corresponding payoffs creates a Nash equilibrium.

**Definition 2.0.4.** A *Nash equilibrium* in a two-person game with strategy sets  $X$  and  $Y$  is a strategy point  $(\hat{x}, \hat{y}) \in X \times Y$  such that

$$\begin{cases} \pi_1(x, \hat{y}) \leq \pi_1(\hat{x}, \hat{y}) \forall x \in X \\ \pi_2(\hat{x}, y) \leq \pi_2(\hat{x}, \hat{y}) \forall y \in Y \end{cases}$$

where  $\hat{x}$  and  $\hat{y}$  can be either pure or mixed strategies. In other words,  $\hat{x}$  and  $\hat{y}$  are best responses to one another. Meaning, if any player cannot gain a better payoff by changing their strategy while knowing the strategies of the other player, the strategy point is a Nash equilibrium.

The beautiful part of the Nash equilibrium concept is that it can be generalized up to  $N$ -person games, where  $N \in \mathbb{R}$ . But before showing the proof for the  $N$ -person case, the following theorem by Brouwer (1911) is needed.

**Theorem 2.0.1 (Brouwer's fixed point).** Suppose that a function  $f : \mathbf{B}^n \rightarrow \mathbf{B}^n$ , where  $\mathbf{B}^n = \{x \in \mathbb{R}^n : |x| \leq 1\}$ , is continuous. Then  $f$  has a fixed point (there is  $a \in \mathbf{B}^n$  such that  $f(a) = a$ ).

For the proof of this theorem, we refer the reader to Kellogg *et al.* (1976) for an inclusive proof written in English, whereas the original proof by Brouwer is in German.

**Theorem 2.0.2. (Existence of Nash Equilibrium Points)** Every  $N$ -person game with finitely many pure strategies has at least one Nash equilibrium if mixed strategies are allowed.

The proof for  $N$ -person case proves both arguments; existence of Nash equilibrium and it holds up to  $N$ -person.

*Proof.* The proof showed here is for the case  $N = 2$  but is readily generalized to any number of players.

Let  $x_1, x_2, \dots, x_m$  and  $y_1, y_2, \dots, y_m$  be pure strategies for the row- and column-player, and let  $x = (p_1, \dots, p_m) \in X$  and  $y = (q_1, \dots, q_m) \in Y$  be mixed strategies. Define the functions

$$\begin{aligned} c_i(x, y) &= \max\{0, \pi_1(x_i, y) - \pi_1(x, y)\} \\ d_i(x, y) &= \max\{0, \pi_2(x, y_i) - \pi_2(x, y)\} \end{aligned}$$

and

$$f(x, y) = \begin{pmatrix} f_X(x, y) \\ f_Y(x, y) \end{pmatrix} = \begin{pmatrix} \frac{p_1 + c_1(x, y), \dots, p_m + c_m(x, y)}{1 + \sum_i c_i(x, y)} \\ \frac{q_1 + d_1(x, y), \dots, q_m + d_m(x, y)}{1 + \sum_i d_i(x, y)} \end{pmatrix}$$

We claim that  $f$  has a fixed point  $(\hat{x}, \hat{y}) \in X \times Y$  and this fixed point is an Nash equilibrium.

To point out that  $f$  has a fixed point, note that  $X$  and  $Y$  are convex sets, and so is the Cartesian product  $X \times Y$ . Moreover,  $f_X(x, y)$  and  $f_Y(x, y)$  are probability distribution over  $x_1, \dots, x_m$  and  $y_1, \dots, y_m$ , and so  $f$  takes values in  $X \times Y$ . Finally, as  $f$  is clearly continuous, we can apply Brouwer's fixed point theorem.

To show a fixed point of  $f$  is a Nash equilibrium, we prove that  $\pi_1(x, \hat{y}) \leq \pi_1(\hat{x}, \hat{y}) \forall x \in X$ . (The proof for the case  $\pi_2(\hat{x}, y) \leq \pi_2(\hat{x}, \hat{y}) \forall y \in Y$  is done similarly as above.)

Write  $\hat{x} = (\hat{p}_1, \dots, \hat{p}_m)$ , and take  $i_0 \in \{1, \dots, m\}$  such that  $c_{i_0}(\hat{x}, \hat{y}) = 0$ . Note that such  $i_0$  must exists, because if it did not, then  $c_i(\hat{x}, \hat{y}) > 0 \forall i$ , i.e.,  $\pi_1(x, \hat{y}) > \pi_1(\hat{x}, \hat{y}) \forall i$ , and so  $\pi_1(\hat{x}, \hat{y}) = \sum_i \hat{p}_i \pi_1(x_i, \hat{y}) > \sum_i \hat{p}_i \pi_1(\hat{x}, \hat{y}) = \pi_1(\hat{x}, \hat{y})$ , which is a contradiction.

Since  $(\hat{x}, \hat{y}) = f(\hat{x}, \hat{y})$ , we have

$$\hat{p}_{i_0} = \frac{\hat{p}_{i_0} + c_{i_0}(\hat{x}, \hat{y})}{1 + \sum_i c_i(\hat{x}, \hat{y})} = \frac{\hat{p}_{i_0}}{1 + \sum_i c_i(\hat{x}, \hat{y})}$$

and so  $\sum_i c_i(\hat{x}, \hat{y}) = 0$ . Since by definition the  $c_i$  are non-negative, it follows that  $c_i(\hat{x}, \hat{y}) = 0$ , i.e.,  $\pi_1(x_i, \hat{y}) \leq \pi_1(\hat{x}, \hat{y}) \forall i$ . Hence, for arbitrary  $x = (p_1, \dots, p_m) \in X$  we have

$$\pi_1(x, \hat{y}) = \sum_i p_i \pi_1(x_i, \hat{y}) \leq \sum_i p_i \pi_1(\hat{x}, \hat{y}) = \pi_1(\hat{x}, \hat{y})$$

which is what we set to prove.  $\square$

The Nash equilibrium expresses a more subtle idea, a more optimistic way of predicting the future where other players make rational moves, what is best for the future at a population level, and assume it is common knowledge for other players also to do so. This expression is based on the assumption that every player in the game has complete information about every move.

Every game cannot be of complete information; each player may have different subjective tastes about the moves available. Another problem comes from arriving at the equilibrium for the players, and why should they play equilibrium strategies, and how is it chosen from all the other equilibria available. There is an example by Aumann (1990) of players having an agreement to play certain Nash equilibrium, among multiple Nash equilibria, but it does not increase the probability of its being played. Subjectivity is always hard to take into consideration, although it affects the decisions of the individual, it can be overlooked if population is the main examination.

A beautiful application of Nash equilibrium points is its use in evolutionary game theory and evolutionary biology. Strategies and behavior evolve over generations, both in human and animal populations. A few examples are animal conflicts, invading living space from another species, apex predator-predator-prey connection and balance, distribution of seeds of plants, and distribution of vaccines in the fight against the viruses. These subjects are discussed in the adaptive dynamics section of this thesis.

## 2.1 Replicator equation

Evolution works by two mechanisms; mutation and selection. Mutation brings variety to the population, whereas selection favors some types over the other. The replicator dynamics describes the evolution of the frequencies of strategies in a population, giving more attention to the role of selection over the role of mutation.

Replicator dynamics presumes that individuals in the population can only choose or be programmed to choose pure strategies. (Mixed-strategist replicator dynamics are studied, for example, by Bomze (1991) and Akin (1982).) Instead of interpreting a mixed strategy as a way of randomization, performed by every individual in the population, where a mixed strategy  $x$  is interpreted as a population state, each component  $x_i$  represents the population share of individuals with pure strategy  $i$ , who are programmed to play a symmetric two-player game. Hence, strategies with lower payoff will vanish.

These dynamics can be considered as the standard population dynamical embedding of games that describes the dynamics of pure strategy frequencies. Let  $x_1, \dots, x_k \in X$  be pure strategies, and let  $p_1, \dots, p_k \geq 0$  with  $\sum_i p_i = 1$  be the corresponding proportion of type  $i$  in a given population. Then the expected payoff to a player with a strategy  $x_i$  against randomly chosen opponent is

$$(2.1) \quad \omega_i \stackrel{\text{def}}{=} \sum_{j=1}^k \pi_1(x_i, x_j) p_j$$

and furthermore the expected payoff to a randomly chosen player against randomly picked opponent is

$$(2.2) \quad \varpi \stackrel{\text{def}}{=} \sum_{i=1}^k \sum_{j=1}^k \pi_1(x_i, x_j) p_i p_j.$$

The replicator equation can be formulated as follows:

$$(2.3) \quad \frac{dp_i}{dt} = p_i(\omega_i - \varpi) \quad (i = 1, \dots, k)$$

which describes the continuous change of the relative frequencies  $p_i$ . This equation itself is a purely frequency-dependent process, which is also its greatest weakness, because almost every time, while analysing populations of any kind, they are regulated by density-dependent processes.

## 2.2 Evolutionarily stable strategy (ESS)

If a sufficiently large population adapts into one strategy, then no other strategy can invade, meaning it cannot increase in frequency within the observed population (Maynard Smith 1982). Consider a large population of individuals or players who encounter randomly chosen opponents. All the strategies available, it is profitable for the individuals to play strict Nash equilibrium<sup>1</sup>, resulting in every other individual deviating from it will be penalized. Hence, such behavior will not spread.

Note: ‘Invasion of one strategy in a population of another strategy’ always depends on the relation of population densities over time and thus the statement is about population dynamics. Therefore, the explicit mathematical conditions for strategy to be an evolutionarily stable strategy depends on the population embedding of the game. This idea can be more elaborated as follows: Let  $x', x \in X$  be two strategies that occur in the population with relative frequencies  $\vartheta$  and  $1 - \vartheta$ , and assume that opponents are assigned randomly so that the probability to be paired with  $x'$ -player is  $\vartheta$ , and probability to be paired with  $x$ -player is  $1 - \vartheta$ . Then expected payoff to an  $x'$ -player is

$$\vartheta\pi_1(x', x') + (1 - \vartheta)\pi_1(x', x)$$

and to an  $x$ -player is

$$\vartheta\pi_1(x, x') + (1 - \vartheta)\pi_1(x, x).$$

Before showing conditions for evolutionary stable strategy, we need to provide the result of Bishop and Cannings (1978, Theorem 1).

**Theorem 2.2.1. (Bishop-Cannings)** If  $I$  is a Nash equilibrium with support<sup>2</sup>  $x_1, x_2, x_3, \dots$ , then  $\pi(x_1, I) = \pi(x_2, I) = \dots = \pi(I, I)$ .

*Proof.* Suppose that  $x_1$  is in the support of  $I$ , and suppose that

$$\pi(x_1, I) < \pi(I, I)$$

Express  $I = \varepsilon(x_1) + (1 - \varepsilon)(X)$  where  $X$  is the strategy, pure or mixed, adopted by  $I$  when it is not  $x_1$ , and where  $\varepsilon$  is the probability of playing strategy  $x_1$ . Then

$$\pi(I, I) = \varepsilon\pi(x_1, I) + (1 - \varepsilon)\pi(X, I) < \varepsilon\pi(I, I) + (1 - \varepsilon)\pi(X, I) < \pi(X, I).$$

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<sup>1</sup>When the inequality, which was shown before as a definition 2.0.4, holds strictly for all players, then it is classified as a strict Nash equilibrium.

<sup>2</sup>If pure strategies  $x_1, x_2, x_3, \dots$  are played with non-zero probability in the mixed strategy  $I$ , then  $x_1, x_2, x_3, \dots$  are said to be in the support of the  $I$ .

But this cannot hold if  $I$  is an Nash equilibrium as we assumed at the beginning. Therefore it cannot be hold true for the case  $\pi(x_1, I) < \pi(I, I)$ . Since  $I$  is an Nash equilibrium, the opposite does not hold either, meaning  $\pi(x_1, I) \not> \pi(I, I)$ . Hence, for any  $x_1$  in the support of  $I$ ,  $\pi(x_1, I) = \pi(I, I)$ , and the theorem is proved.  $\square$

Strategy  $x$  is defined as *evolutionary stable strategy*, if and only if for every  $x \neq x'$  it meets the first-order or the second-order best-reply conditions represented by Maynard Smith and Price (1973):

$$(2.4) \quad \pi_1(x', x) < \pi_1(x, x) \quad \forall x \in X$$

or

$$(2.5) \quad \pi_1(x', x) = \pi_1(x, x) \quad \& \quad \pi_1(x', x') < \pi_1(x, x') \quad \forall x \neq x'$$

Here the first criterion states that if  $x$  is evolutionarily stable, it has to be better reply to  $x'$  than  $x'$  to itself. The latter states, since an ESS corresponds to Nash equilibrium, the Bishop-Cannings theorem holds for it. Although, some rare mutant strategy can cope as well against strategy  $x$  as  $x$  does when playing against itself, but  $x$  fares better playing against the mutant than the mutant does. To put it simply the latter condition: If in a population, where the strategy  $x$  is common, a mutant strategy  $x'$  arises whose payoff against strategy  $x$  is the same as strategy  $x$  against itself, then the mutant strategy  $x'$  will increase in frequency until meetings between two  $x'$  becomes a common event. This remark is useful in the search of mixed ESS candidates, but it does not guarantee stability. It is necessary, when found suitable candidate, to check stability by showing that  $\pi_1(x', x') < \pi_1(x, x')$  holds for all  $x'$ , where  $x'$  can be mixed or pure strategy.

**Example 2.2.1.** Let us write a payoff matrix, which reminds a bit of Hawk-Dove matrix, to utilize the Bishop-Cannings theorem in search for the ESS

	$H$	$D$
$H$	$a$	$b$
$D$	$c$	$d$

If  $a > c$  then H is an ESS.

If  $d > b$  then D is an ESS.

If both inequalities hold, then H and D are both ESS's.

We are left with cases where  $a < c$  and  $d < b$ . Let  $I$  be mixed strategy, same as before, expressed as  $\varepsilon(H) + (1 - \varepsilon)(D)$ , where  $\varepsilon$  is the probability to play strategy H. If  $I$  is an ESS, then by Bishop-Cannings theorem

$$a\varepsilon + b(1 - \varepsilon) = c\varepsilon + d(1 - \varepsilon).$$

If  $a < c$  and  $d < b$ , there exists always a solution to this equation with  $0 < \varepsilon < 1$ . The solution is

$$\varepsilon = \frac{(b-d)}{(b-d)+(a-c)}$$

To show that this solution is stable, consider an alternative strategy expressed as  $J = \varphi(H) + (1 - \varphi)(D)$ , where  $\varphi$  behaves similarly as  $\varepsilon$ . Since the strategy  $I = \varepsilon(H) + (1 - \varepsilon)(D)$  has the property, by Bishop-Cannings theorem, that  $\pi(H, I) = \pi(D, I)$ , it follows that  $\pi(J, I) = \pi(I, I)$ . Hence  $I$  will be stable if  $\pi(I, J) > \pi(J, J)$ . Now

$$\begin{aligned}\pi(I, J) - \pi(J, J) &= \pi(I, J) - \pi(I, I) + \pi(\varphi, I) - \pi(J, J) \\ &= (I - J)^2(b + c - a - d)\end{aligned}$$

Since  $c > a$  and  $b > d$  and  $I \neq J$ , it follows that  $\pi(I, J) > \pi(J, J)$ , and hence  $I$  is stable.

Hence H is an ESS, or D is an ESS, or both H and D are ESS's, or there is a mixed ESS.

**Theorem 2.2.2.** If a game has two ESSs, then the support of the one cannot be a subset of the other.

*Proof.* Let  $\hat{x}_1$  and  $\hat{x}_2$  be two evolutionary stable strategies. To reach a contradiction, suppose that the support of  $\hat{x}_1$  is a subset of the support of  $\hat{x}_2$ . Then, by the Bishop-Cannings theorem, it follows  $\pi_1(\hat{x}_1, \hat{x}_2) = \pi_1(\hat{x}_2, \hat{x}_2)$ , and so the first ESS condition fails for  $\hat{x}_2$ . Hence, the second ESS condition should hold, i.e.,  $\pi_1(\hat{x}_1, \hat{x}_1) < \pi_1(\hat{x}_2, \hat{x}_1)$ . But this contradicts that  $\hat{x}_1$  too, is an ESS.  $\square$

This convenient result saves time and trouble of checking for the existence of all the possible ESS's. Whenever there exists an ESS with full support in a given game, then that ESS is the only possible one for that game.

## 2.3 Iterated game

A tried and tested way to add spice to a game is to repeat it. Games with multiple rounds (or stages) are called iterated games. They have either infinitely many rounds or countable many rounds. Here, for simplicity, we assume the same strategy sets  $X_1 = X_2 = \dots$  and  $Y_1 = Y_2 = \dots$  for each round.

The payoff what player can get from repeated games is just the sum of every one-round game played repeatedly over several rounds varying from  $0, 1, \dots, n, \dots, N$  where  $N$  is the total number of rounds and  $n$  is  $n$ :th round of the game. In each round, every player executes a certain amount of actions between other players, and payoffs for each player are decided by the strategy they are using against other players. The set up here is the same for the payoffs, and player actions as shown before.

If a smaller segment of the iterated game is under consideration, it is called a subgame. When in isolation, a subgame constitutes a game in its own right. All the same properties, as in a regular game, holds for the subgames. Hence, Nash equilibrium can be defined for each subgame separately. Although, the subgame concept is mostly used in perfect information games with finitely many rounds (Selten 1965; Kohlberg and Mertens 1986, pp. 1013-1026). If the whole game has a unique Nash equilibrium, then the repeated game has a unique subgame perfect Nash equilibrium strategy of playing the one round game equilibrium in each round (Osborne 2003, pp. 162-165). An example of this type of scenario is a finitely repeated Prisoner's dilemma. To minimize the time spent in jail, both players will *Defect*, which is also one-round unique Nash equilibrium. The same result is obtained by backward

induction<sup>3</sup>; it is profitable to play Nash equilibrium in the last round of the game. Therefore, it is in the players' best interest to play Nash equilibrium in the second-to-last round of the game, in the pursuit of maximum payoff (or in this case, more like risk-avoiding action, in fear of prolonged time in prison). Hence, players should always play *Defect* over *Cooperation*.

Depending on the number of rounds, alternative strategies can be completely viable options for maximum payoff. If a player can spot a pattern in opponents' actions, picking the more irrational or questionable strategy might yield a better payoff than choosing the more recognizable strategy (Suzuki and Akiyama 2007). This only works when players do not have an equal understanding of the information of the game. Players can value moves in the game differently, having motives behind their actions or subjectivity affecting the decisions.

Let us focus on a Hawk-Dove game with multiple rounds more closely, and different strategies that can coexist within the population. Being a Hawk-player can be considered an ESS if the cost of hurting yourself in battle with another Hawk-player is low enough. Increasing the cost of an injury endured in a battle makes these games much more interesting because players then must adapt their strategies round per round basis to achieve the maximum payoff. Some examples of different strategies are Bully: plays Hawk against Dove, but crinkles against Hawk and plays Dove; Retaliator: plays Dove against Dove, but plays Hawk when facing Hawk. Every one of these strategies can attain a dominant position in the population in iterated games if a pool is taken into consideration (Ollikainen 2018). To briefly define the pool, it is a waiting room for inactive players who are not in the game currently. Players get picked out from the pool with some probability and are paired to play against each other. After the game is over, players return to the pool and wait until they get paired against next opponent. Accepting quitting as a strategy, or part of a strategy, it readjusts the function of the pool. When the payoff, after the round ends, does not match the motives of a player, payoff being lower what anticipated, quit the game and return to the pool as a inactive player. This matter is discussed more thoroughly in the fourth chapter.

**Example 2.3.1.** Recall the Prisoner's Dilemma with the payoffs  $T > R > P > S$  now corresponding to the fixed values shown in the example previously. Here the strategy *Defect* (D) is a strictly dominating strategy, and therefore (D,D) is the dominating strategy solution, even though both players would have higher payoffs if they played *Cooperation* (C,C).

The question now is whether the strategy *Defect* (D) remains dominant if the game is played multiple rounds as in iterated games. The answer here depends on the number of rounds and does the players know beforehand how many rounds they are going to play. If the Iterated Prisoner's Dilemma (IPD) is played  $N$  times, where  $N$  is fixed number, and both players know this, then the strategy *Defect* is still dominant. The proof for this claim comes quite straightforwardly by backward induction: *Defect* is dominant in the last round, and therefore both players will *Defect* on the round  $N$ . Given that *Defect* is dominant on the round  $N$ , *Defect* is therefore also dominant in the second-to-last round  $N - 1$ , and so both players will *Defect* on  $N - 1$  round. This reasoning holds until the first round. The same applies as long as the upper limit of rounds is known for both players.

*Cooperation* challenges the dominant strategy *Defect* if the total number of rounds  $N$  is

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<sup>3</sup>Nöldeke and Samuelson (1993) did an interesting study of evolutionary analysis of backward and forward induction. They examined games where backward induction works: finite extensive form games of perfect information. Whereas forward induction played a much larger role in the evolutionary approach to games.

random or unknown to the players. Therefore players must assume that there exists some probability of a further round. Defection in this scenario would be foolish and yield immediate gain in the present round only, but demolish any hope of cooperation in the coming rounds. (Assuming that you play against the same opponent every round until the iterated game ends.) Continued by defecting, it is followed up with a loss that cannot be compensated by the short-term gain in one round. *Cooperation* becomes a more tempting and sustainable strategy in the long run (Aumann 1959). Another factor, which plays a role in the evolution of cooperative behavior, is the relation between the payoffs. If the payoff of defecting against the cooperator is small compared to the net benefit of cooperation, then the cooperation is favored in the iterated games (Fogel 1993, pp. 94-95).

The common way to implement a random game length is to assume constant probability  $\delta \in (0, 1)$  that there is a another round after the current one. Therefore the total number of rounds is a random variable with a geometric probability distribution and expected value

$$1 + \delta + \delta^2 + \delta^3 + \dots = \frac{1}{1-\delta}$$

Here we can then distinguish either fixed strategies, random strategies or rule-based strategies. Few examples for fixed strategies are:

1. *allD* = (D, D, D, D, ...)
2. *allC* = (C, C, C, C, ...)
3. *Alternate* = (C, D, C, D, ...)

A random strategy is just a sequence  $(d_1, d_2, d_3, \dots)$  where  $d_n \in [0, 1]$  is the probability of choosing D instead of C in the  $n^{th}$  round. Here it is clear that fixed strategies form a subset of the random strategies.

In a rule-based strategy, the line of action depends on the history of the game up that moment and the length of the memory that the players have. However, it is more convenient to assume memory of length one to keep the calculations manageable. For example, ‘Tit for tat’ (TFT): “*Choose C in the first round; after that choose whatever your opponent played in the previous round.*” Playing TFT against a hypothetical opponent could look something like this:

<b>TFT:</b>	.. C D D D C D C C C D D ..
<b>opponent:</b>	.. C D D D C D C C C D D ..

TFT rewards the cooperation with cooperation and punishes defection with defection.

Tit for tat as a strategy in iterated Prisoner’s dilemma game has its history. A tournament kept in 1979 by young American professor Robert Axelrod invited everyone interested to submit a strategy for iterated Prisoner’s dilemma game. Fifteen participants sent in their proposal, and they were analyzed on the computer. Proposal submitted by Anatol Rapoport, a strategy called tit for tat, won the whole tournament by superb pedigree (Axelrod 1980). The result might come as a surprise because tit for tat did not win a single match. The strength of this strategy is that you can earn as many points as your opponent, or even less,



but not more. In this sense, tit for tat is a good strategy because it is never very far behind, but it is never out in front either.

After the tournament, there came into existence different variations of tit for tat. One of them was *tit for two tats* - a strategy which only defects if the opponent has defected two times in a row. Another variation is *tit for tat with forgiveness* - behaves like the original one, but instead of answering defection with defecting, with a small probability, it will play cooperation instead. Axelrod, called for another tournament, and once again Rapoport submitted tit for tat, which won against sixty-two other strategies (Axelrod 1984).

Another example of a rule-based strategy is ‘Pavlov’: “*Choose C in the first round; after that repeat the same action as in the previous round if your payoff was high (for example, R or T); otherwise change.*” Pavlov against the same opponent as above thus looks like:

**Pavlov:**     .. D D C D C C D D D D C ..

**opponent:** .. C D D D C D C C C D D ..

Pavlov can be described as a ‘win-stay, lose-switch’ strategy. The choices what to play change accordingly to what Pavlov considers as a high enough payoff.

Tit for tat and Pavlov are both so-called memory-1 strategies, these strategies can only use the information shown one round before to make up the decision for current round.

There exists another approach to modeling games, which is not that common in the literature of game theory, but an interesting one for sure: Quitting. In iterated games, quitting can be more efficient than staying in the game as a whole, for example, if player’s payoff for each round is negative, quitting and finding a new opponent can yield more beneficial match-up for the player. This strategy can be executed in situations where the payoff does not match with the player’s motives or if the total payoff is too low. In this case, it should yield some negative effect on the player to quit and find a new player because without any sanctions dominant strategy would be to quit as long as you find a player with whom match-up gives you the maximum payoff. One solution for this would be tournament-type rules, where you are playing against other players with the same record (Win-Lose-Draw).

Another way is to assume that quitting and then finding a new player takes time measured in several rounds, for example, one to three rounds. Then your overall payoff can be either reduced significantly or increased depending on the current match-ups and the potentiality of quitting in hopes of finding better match-up. One real-life example, what I thought of, could be the game of Work and Education: Player’s payoff is calculated by how well the attributes, given by the education, are used in the ongoing work. Does there exist a better work position for the individual that would reflect the skill set acquired by the education? In cases when there exists a better opportunity for the individual, is it still worth the risk of quitting the current work and change it in the hopes of a better one? This examination can act as a population-level diagnosis, where a sufficiently large part of the population are in sub-optimal work. It decreases the whole populations’ ability to compete with others. The measurement unit in this inquiry could be the nation’s GDP or overall happiness based on a respondent rating of their own lives.

# Chapter 3

## Adaptive Dynamics

Adaptive dynamics<sup>1</sup> is a conceptual and mathematical framework for modelling long-term evolution by mutation and natural selection in potentially complicated ecological systems. The basic idea is simple: we start with a population of one or more interacting species<sup>2</sup> each characterised by a unique morphological trait or behavioural strategy<sup>3</sup>. We call this the resident population. Next, we introduce a new species with an altogether different strategy at an initially very low population density. We call this a mutation event, and the new species we call the mutant. We are concerned with the following two questions:

**Q1.** Can the mutant invade (i.e., increase in population density) and if so, what will be the consequences in terms of which species (possibly including the mutant) will survive and which will go extinct following the ecological upheaval due to the arrival of the newcomer?

**Q2.** What will be the long-term consequences of many successive distinct invasion-extinction events in terms of changes in the strategy composition of the population?

The first question is about natural selection as an emergent property of the underlying population dynamics. The second question is about long-term evolution, which does not play in the population state space but in different space altogether, namely, the space of finite subsets of the set of all possible strategies. The objective of adaptive dynamics is to understand long-term evolution as an emergent process of the mutation and (through selection) population dynamics. To simplify the task of mathematical modelling and subsequent analysis we make the following assumptions:

**A0.** The dynamics of the resident population has a unique and strictly positive attractor<sup>4</sup> for the population densities.

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<sup>1</sup>Pioneered by Metz *et al.* (1996) and Geritz *et al.* (1997, 1998, 1999)

<sup>2</sup>Here we use the word “species” not in the biological sense but more as a physicist uses it when referring to different kinds of particles.

<sup>3</sup>We will use the term “strategy” to refer to a morphological trait or a behavioural strategy depending on the context.

<sup>4</sup>An attractor is a non-empty compact subset  $A$  of the state space such that  $A$  is forward invariant under the dynamics of the system, and  $A$  has an open neighbourhood  $B$  such that every forward orbit starting in  $B$  converges to  $A$ , and no non-empty proper subset of  $A$  has the first two properties.

**A1.** Mutation is a very slow process relative to the resident population dynamics so that mutations happen only infrequently and we need to consider only one mutation event at a time.

**A2.** The initial population density of the mutant is so small that invasion becomes a mere matter of boundary stability in the combined resident-mutant population state space where the resident attractor is now embedded in the boundary manifold where the density of the mutant is zero.

**A3.** Evolution proceeds by small steps, i.e., the strategy of the mutant is always chosen from within a small neighbourhood of one of the resident strategies. This allows us to develop a local (in strategy space) and virtually application-independent theory of adaptive dynamics.

Next, we show how the above ideas can be mathematically implemented given a system of equations for the resident dynamics. We will confine ourselves to one-dimensional strategies<sup>5</sup> and unstructured populations with dynamics that are described by an autonomous system of ordinary differential equations with a unique and strictly positive attractor for the population densities. For generalizations including multi-dimensional strategies, structured populations with dynamics described by other kinds of equations, and possibly with multiple population attractors, we refer to the website <https://www.mv.helsinki.fi/home/kisdi/addyn.htm> for more information.

### 3.1 Resident dynamics

Consider a resident population with strategies  $x_1, \dots, x_k \in \mathbb{R}$  and corresponding population densities  $n_1(t), \dots, n_k(t) \in \mathbb{R}_+ \cup \{0\}$  in the environment  $e(t) \in \mathbb{R}^l$  at time  $t \geq 0$ . The resident dynamics are given by

$$(3.1) \quad \begin{cases} \dot{n}_i(t) = f(x_i, e(t))n_i(t) & i = 1, \dots, k \\ \dot{e}(t) = g(e(t)) + \sum_{j=1}^k h(x_j, e(t))n_j(t), \end{cases}$$

for appropriate initial conditions, and where the dot denotes differentiation with respect to time variable  $t$ . The  $f(x_i, e(t))$  is the per-capita growth rate for strategy  $x_i$  in the environment  $e(t)$ . The function  $g(e(t))$  describes the intrinsic dynamics of the virgin environment (the environment unaffected by the population with strategies  $x_1, \dots, x_k$ ). The  $h(x_j, e(t))$  is the per-capita environmental impact for strategy  $x_j$  in the environment  $e(t)$ . By assumption **(A0)**, the dynamics of (3.1) has a unique attractor where, moreover, all population densities  $n_i$  are strictly positive.

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<sup>5</sup>Such as bill length in birds, or amount of fat reserve as a percentage of total body weight, etc., as examples of one-dimensional morphological traits, and the probability of escalating a conflict with a competitor instead of retreating, or the probability of confiscating a nest from a conspecific instead of building one yourself, etc. as examples of one-dimensional behavioral strategies.

## 3.2 Resident-mutant dynamics

We now consider the effect of introducing a mutant strategy. By assumption **(A1)** we need to consider only one new mutant strategy at a time. Introduction of a mutant strategy  $y \in \mathbb{R}$  with the corresponding population density  $m(t) \in \mathbb{R}_+ \cup \{0\}$  for time  $t \geq 0$ , leads to the combined resident-mutant dynamics given by

$$(3.2) \quad \begin{cases} \dot{n}_i(t) = f(x_i, e(t))n_i(t) & i = 1, \dots, k \\ \dot{m}(t) = f(y, e(t))m(t) \\ \dot{e}(t) = g(e(t)) + \sum_{j=1}^k h(x_j, e(t))n_j(t) + h(y, e(t))m(t), \end{cases}$$

Note that there is no structural difference between the equations for the residents and the mutant. By assumption **(A2)**, the population density  $m$  of the mutant is very much smaller than that of the resident. In the limit for  $m \rightarrow 0$  the environment  $e(t)$  no longer depends on the mutant, and so for the densities  $n_1(t), \dots, n_k(t)$  we recover the resident dynamics (3.1) while for the mutant  $m$  we get

$$(3.3) \quad \dot{m}(t) = f(y, e(t))m(t),$$

where  $e(t)$  is the environment by the resident system (3.1). In other words, the resident dynamics including the environment remain unaffected by the introduction of an initially rare mutant strategy. Figure 3.1 shows the relationship of the mutant  $(y, m(t))$  and the resident system  $(x_1, \dots, x_k, n_1(t), \dots, n_k(t), e(t))$  where arrows with the functions shown in the dynamics (3.2) illustrate different impacts or contributions between them.

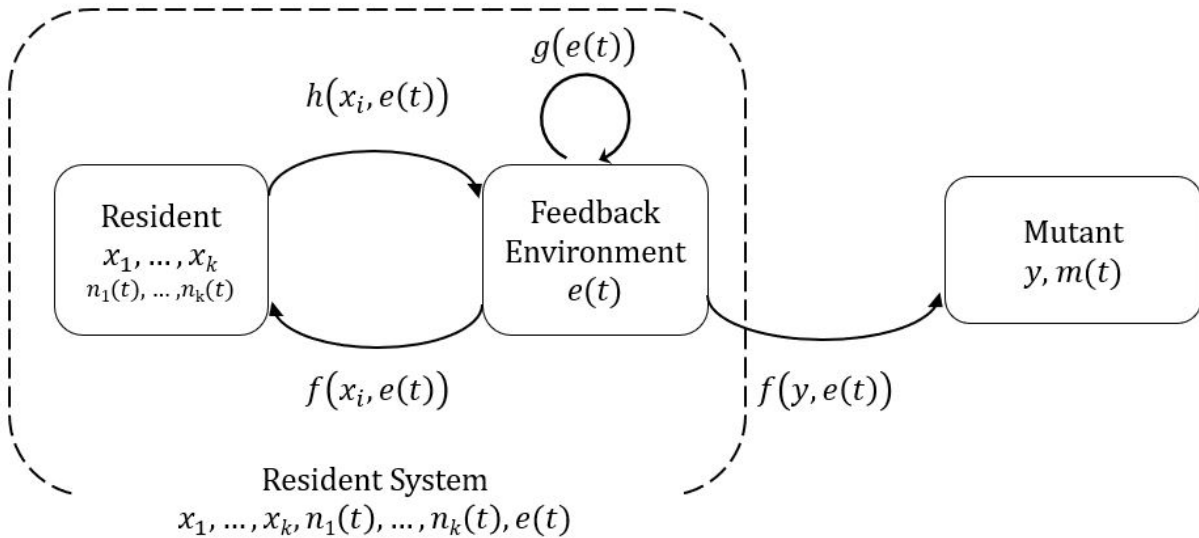


Figure 3.1: Diagram of the interaction between the resident population and the feedback environment and the one-directional impact on the mutant population. (The original figure, which this figure resembles, is from article by Cai and Geritz (2020, Figure 1).)

### 3.3 Invasion and invasion fitness

We now are able to answer the question **Q1** in section 3.1. Solving equation (3.3) for the population dynamics of the mutant, we find

$$(3.4) \quad \log m(t) = \log m(0) + t \langle f(y, e(\tau)) \rangle_{\tau=0}^t,$$

where

$$(3.5) \quad \langle f(y, e(\tau)) \rangle_{\tau=0}^t = \frac{1}{t} \int_0^t f(y, e(\tau)) d\tau$$

is the average mutant's per-capita growth rate over the time interval  $(0, t)$ . We define the *invasion fitness*  $s_e(y)$  of strategy  $y$  in the environment  $e : \mathbb{R}_+ \rightarrow \mathbb{R}^l$  as the long-term time average of the mutant's per-capita growth rate, i.e.,

$$(3.6) \quad s_e(y) = \lim_{t \rightarrow \infty} \langle f(y, e(\tau)) \rangle_{\tau=0}^t$$

provided the limit exists and is independent of  $m(0) > 0$ . Then we can conclude that

1.  $s_e(y) > 0 \implies \lim_{t \rightarrow \infty} m(t) = \infty$  ("strategy  $y$  invades the environment  $e(t)$ ")
2.  $s_e(y) < 0 \implies \lim_{t \rightarrow \infty} m(t) = 0$  ("strategy  $y$  does not invade the environment  $e(t)$ ")

The case  $s_e(y) = 0$  remains undetermined: the mutant  $y$  may grow or decline but in both cases at a sub-exponential rate<sup>6</sup>.

Positive invasion fitness alone does not tell the whole story, i.e., what happens after the invasion event. Remark that in general the invasion itself does not imply which species (possibly including the mutant) will survive and which will go to extinct following the ecological upheaval due to the arrival of the newcomer. In the case of small mutations steps **(A3)**, the invasion implies substitution of or coexistence with the resident type it was derived from, depending on whether or not the latter can invade a population in which the resident is replaced by its mutant (Geritz 2005, Dercole and Geritz 2016). With small mutations **(A3)**, we can use the selection gradient to know into what direction (in strategy space) the population will evolve. The selection gradient  $D(x)$  is defined as

$$(3.7) \quad D(x) = \left. \frac{\partial s_e(y)}{\partial y} \right|_{y=x}$$

The invasion fitness of each resident strategy is zero, i.e.,  $s_e(x_i) = 0$  for all  $i$ . This we refer to as the *principle of selective neutrality of the residents*. To see why this is so, recall from the resident dynamics (3.1) that  $\dot{n}_i(t) = f(x_i, e(t))n_i(t)$ , from which we solve

$$\log n_i(t) = \log n_i(0) + t \langle f(x_i, e(\tau)) \rangle_{\tau=0}^t.$$

Division by  $t$  and letting  $t \rightarrow \infty$  we get  $s_e(x_i) = 0$ , because from assumption **(A0)** it follows that  $\log n_i(t)$  is bounded on forward orbits. Then it follows that the sign of  $D(x)$  determines what mutants can invade **(A2)**. If  $D(x) > 0$ , then mutants with  $y > x$  can invade, whereas if  $D(x) < 0$ , only mutants with  $y < x$  can invade. A strategy for which the selection gradient vanishes is called a singular strategy (or alternatively a singular point).

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<sup>6</sup>Here we model the resident and mutant dynamics in the same system as in (3.2). Alternatively, one can model the mutant dynamics separately as a stochastic branching process for a finite number of individuals, in which case  $s_e(y) = 0$  is not indeterminate but leads to extinction with probability one. (Geritz *et al.* 2018)

### 3.4 Evolutionarily- and Convergence stable strategies

We now are able to answer the question **Q2** in section 3.1. Once the invasion fitness and selection gradient is well defined, singular strategies can be analyzed further. First, it is essential to find those points where selection gradient vanishes, that is,  $D(x^*) = 0$  holds, where  $x^* \in \mathbb{R}$ . The intriguing question here is: How does the population, which is at a singular point  $x^*$ , behave against the mutant population with a strategy close to singular point (**A3**)?

Assume an unbeatable strategy in the resident population. When vast majority of the individuals has this strategy, no mutant with different strategy can successfully increase in numbers (Maynard Smith 1982). Such a population is evolutionarily stable when no new mutants can invade the population. The condition for strategy  $x^*$  to be *evolutionarily stable strategy* (Geritz *et al.* 1998, p. 38) is the following:

$$(3.8) \quad \left. \frac{\partial^2 s_e(y)}{\partial y^2} \right|_{y=x=x^*} < 0,$$

which is a (local) maximum of  $s_e(y)$ . Evolutionary stable strategy is, in a sense, an endpoint to evolution: when a population has reached this particular state, the possibility of an invasion by mutant has vanished. Small mutations cannot change the current state of the population.

If the resident population has a strategy  $x$ , which is near the singular point  $x^*$ , will mutants that are able to invade be closer to  $x^*$  – that is, if  $s_e(y) > 0$  for  $x < y < x^*$  and  $x^* < y < x$ . If the answer is yes, it indicates that the singular point is (locally) *convergence stable strategy* (or convergence-stable). In other words, the selection gradient is positive for all  $x < x^*$  and negative for all  $x > x^*$ . Since  $x^*$  is the point where the sign of the selection gradient changes from positive to negative,  $D(x)$  is a locally decreasing function of  $x$ . The conditions for convergence stability are given as

$$(3.9) \quad \frac{\partial D(x)}{\partial x} = \left. \frac{\partial^2 s_e(y)}{\partial x \partial y} \right|_{y=x=x^*} + \left. \frac{\partial^2 s_e(y)}{\partial y^2} \right|_{y=x=x^*} < 0,$$

which can be rewritten if we consider two useful identities

$$\frac{\partial s}{\partial x} + \frac{\partial s}{\partial y} = 0,$$

and therefore it holds for

$$(3.10) \quad \frac{\partial^2 s}{\partial x^2} + 2 \frac{\partial^2 s}{\partial x \partial y} + \frac{\partial^2 s}{\partial y^2} = 0.$$

If we use the upper equation to eliminate the cross-derivative in (3.9), we get more sophisticated form

$$(3.11) \quad \left. \frac{\partial^2 s_e(y)}{\partial y^2} \right|_{y=x=x^*} < \left. \frac{\partial^2 s_e(y)}{\partial x^2} \right|_{y=x=x^*}.$$

A singular strategy  $x^*$  that is convergence stable is an evolutionary attractor, for a monomorphic population. On the contrary, if the singular strategy  $x^*$  is not convergence stable, then it is an evolutionary repeller from which a monomorphic population will evolve away.

If the singular strategy is both evolutionarily - and convergence stable, it is called continuously stable strategy (CSS<sup>7</sup> as a abbreviation, but it can be confused with convergence stable strategy).

Consider a singular point that is an evolutionarily stable, but not convergence stable. This configuration is referred to as Garden-of-Eden (Nowak and Sigmund 1990). Even though the resident with the singular strategy cannot be invaded by any mutants nearby, the resident population will evolve further away from the singular point if it is arbitrarily close but not equal to the singular point.

Other way around is also possible: a singular point that is convergence stable, but not evolutionarily stable. The population converges towards the singular point, and once they have reached it, this leads the population to be vulnerable to invasions by mutants nearby. In this case, the singular point is a minimum for the invasion fitness function. Therefore, convergence into such a point opens the opportunity for coexistence of similar strategies (Geritz *et al.* 1998, p. 42).

### 3.5 Evolutionary Branching

The anticipated outcome of a successful invasion event leads the mutant to replace the resident population. If the successful mutant cannot oust the former resident completely, the result then is a coexistence of two subpopulations. Therefore, the population becomes dimorphic.

First, before rise of the dimorphic population, there must exist two strategies  $x \in \mathbb{R}$  and  $y \in \mathbb{R}$  arbitrarily close to singular strategy  $x^*$  such that the invasion fitness for both strategies are positive,  $s_e(y) > 0$  and  $s_e(x) > 0$ , in the neighborhood of  $x^*$ . Here we say that  $y$  and  $x$  can *mutually invade*. Since the  $s_e(y)$  has a local minimum for  $y = x = x^*$ , the second-order derivative must be positive, that is,

$$(3.12) \quad \frac{\partial^2 s_e(y)}{\partial x^2} - 2 \frac{\partial^2 s_e(y)}{\partial x \partial y} + \frac{\partial^2 s_e(y)}{\partial y^2} > 0.$$

If we apply equation (3.10) to eliminate the cross-derivative as before, we find

$$(3.13) \quad \left. \frac{\partial^2 s_e(y)}{\partial x^2} \right|_{y=z=x^*} > - \left. \frac{\partial^2 s_e(y)}{\partial y^2} \right|_{y=z=x^*}$$

as a necessary condition for mutual invasibility (Geritz *et al.* 1998, p. 40). Once the initially monomorphic population can satisfy the condition above, it can become dimorphic in the neighborhood of singular strategy  $x^*$  with small evolutionary steps (**A3**). (Observe that (3.13) holds whenever the singularity is convergence stable (3.11), and lacks the evolutionary stability (3.8).) In these points  $x^*$  where the fitness gradient vanishes, the resident-mutant dynamics are ruled by the *selection curvatures*, which are the second-derivatives of the invasion fitness with respect to resident and mutant strategies (**A2**).

The evolutionary significance of mutual invasibility depends on the convergence stable singular strategy  $x^*$  and whether it is or not an evolutionary stable. If  $x^*$  is an evolutionary stable and convergence stable strategy, then mutually invisable strategies are positioned on

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<sup>7</sup>Eshel 1983, p. 101

the opposite sides of the singular strategy  $x^*$ . The mutant with a strategy  $y$  has a negative fitness elsewhere but one point, and it reaches its maximum value at that point  $y = x^*$  where it is zero by the definition.

In a dimorphic case, where a mutant with a strategy  $y$  can invade the resident population with strategies  $x_1$  and  $x_2$  (with  $x_1 < x_2$ ) if, and only if,  $x_1 < y < x_2$ . The resident population have strategies  $x_1$  and  $x_2$  in the opposite sides of the near singular strategy  $x^*$ , which is evolutionary stable and convergence stable. The invasion fitness for the mutant is zero at the points  $y = x_1$  and  $y = x_2$ , and therefore by continuity, it reaches its maximum value in the interval  $]x_1, x_2[$ , where the fitness is positive (since we assume that the singular strategy  $x^*$  is an ESS, and therefore the invasion fitness of the mutant is concave down). Mutants outside the interval cannot invade, whereas mutants inside it can invade. The population stays dimorphic if, after successful mutant, the resident strategy is on the same side as the mutant, which is near the singular strategy  $x^*$ .<sup>8</sup> The distance between these two strategies narrows eventually, when the population gradually evolves towards the evolutionary stable state (**A3**). This means that any dimorphism is ultimately temporary, and the population will eventually evolve towards the monomorphic ESS  $x^*$ . The term *converging dimorphism* has been used to represent this situation.

In the case of a minimum, where  $x^*$  is convergence stable but not an evolutionarily stable, mutant can invade if, and only if,  $y < x_1$  or  $x_2 < y$ . To emphasize the situation, consider the monomorphic resident population at a singular strategy  $x^*$  that is not an evolutionarily stable strategy (note that then it holds  $\frac{\partial^2 s_e(y)}{\partial y^2}|_{y=x^*} > 0$ ). Therefore, the invasion fitness is concave up and take its minimum value at  $s_e(x^*) = 0$ . Nearby mutants can invade and hence have a positive fitness. A small perturbation pushes the minimum of this curve below the horizontal axis, and then the invasion fitness will have two roots  $x_1$  and  $x_2$  one of either side of  $x^*$ . Only mutants outside the two resident types  $x_1$  and  $x_2$  can invade and have positive fitness, whereas mutants in between cannot. After each successive invasion, the strategy in the middle gets ousted, leading the two remaining strategies to become more distinct from one and another. Ultimately, the population splits up into two diverging subpopulations. This process of interactions of genotype and environment divergence into an initially monomorphic society we call *evolutionary branching*. The singular strategies that enable this process we call *evolutionary branching points*.

To conclude this section, the singular point  $x^*$  is either an endpoint of evolutionary dynamics or an evolutionary branching point. If singular strategies are convergence stable and evolutionarily stable strategies, this brings on steady selection on both monomorphic and nearby dimorphic populations. Therefore, the evolutionary process has reached its endpoint, at least under the assumption of small mutations (**A3**), leading to monomorphic outcomes. If singular strategies are convergence stable but not evolutionarily stable, they repel nearby dimorphic populations further away from each other. On the other hand, they attract monomorphic populations, until it has come sufficiently close to the singular strategy, the group will become dimorphic and face disruptive selection<sup>9</sup>. Inevitable consequence of this is two phenotypically distinct and simultaneously diverging subpopulations. This concludes

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<sup>8</sup>For example, assume that the order is following:  $x_1 < x^* < y < x_2$ , where  $y$  and  $x_2$  are on the same side.

<sup>9</sup>Disruptive selection is a specific type of natural selection that actively selects extreme trait values over favored intermediate trait values. Mather (1955) has studied this phenomenon more thoroughly.



the answers to questions **Q1** and **Q2**.

## 3.6 SI model

### 3.6.1 Resident dynamics and feedback environment

The invasion fitness is the main tool of adaptive dynamics. We will illustrate its use by means of an example. To describe the spread of a pathogen within the resident population, consider the following SI model (susceptible-and-infected model)

$$(3.14) \quad \begin{aligned} \frac{dS}{dt} &= \lambda S - \mu S - \gamma N S - \sum_{j=1}^k \beta(\alpha_j) I_j S \\ \frac{dI_i}{dt} &= -\mu I_i - \gamma N I_i + \beta(\alpha_i) S I_i - \alpha_i I_i \quad \text{for } i = 1, \dots, k, \end{aligned}$$

where the total population density  $N = S + \sum_{i=1}^k I_i$  consist of susceptibles  $S$  and infected with virus strain  $i = 1, \dots, k$  described as  $I_i$ . Susceptibles are born at per capita rate  $\delta$  (only susceptibles reproduce) and die at the per capita rate  $\mu$ . The same per capita death rate  $\mu$  holds for infected individuals as well. Additionally, there is density dependent per capita death rate  $\gamma N$  as well. Infected individuals  $I_i$  encounter and infect susceptibles at strain specific transmission rate  $\beta(\alpha_i)$ , where  $\beta : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ , twice continuously differentiable and monotonically increasing function of virulence. Infected individuals have increased mortality in the form of strain specific virulence  $\alpha_i$ . Note that in this SI model individual does not recover from the disease. Once the individual becomes infected, that individual will permanently carry the pathogen.

By changing notations, we can rewrite the system (3.14) to be similar to the system (3.1). Let  $n_i = I_i$  and  $x_i = \alpha_i$  for  $i = 1, \dots, k$  and  $e = \begin{pmatrix} e_1 \\ e_2 \end{pmatrix} = \begin{pmatrix} S \\ N \end{pmatrix}$ . Then the resident dynamics are given by

$$(3.15) \quad \begin{aligned} \frac{dn_i}{dt} &= f(x_i, e)n_i = (-\mu - \gamma e_2 + \beta(x_i)e_1 - x_i)n_i \quad \text{for } i = 1, \dots, k \\ \frac{de}{dt} &= g(e) + \sum_{i=1}^k h(x_i, e)n_i = \begin{pmatrix} (\lambda - \mu)e_1 - \gamma e_2 e_1 \\ \lambda e_1 - \mu e_2 - \gamma e_2^2 \end{pmatrix} + \sum_{i=1}^k \begin{pmatrix} -\beta(x_i)e_2 \\ -x_i \end{pmatrix} n_i \end{aligned}$$

with initial condition  $e_2(0) = e_1(0) + \sum_{i=0}^k n_i(0)$ .

### 3.6.2 Mutant dynamics and invasion fitness

Next, assume a variant strategy  $y$  with a corresponding population density  $m \in \mathbb{R}_+$  that is introduced into the resident population. The mutant dynamics is then given by

$$(3.16) \quad \frac{dm}{dt} = f(y, e)m = (-\mu - \gamma N + \beta(y)S - y)m,$$

where  $S$  and  $N$  are given by the resident population. The invasion fitness of the mutant  $y$  in the environment generated by the resident population is given by

$$(3.17) \quad s_{S,N}(y) = -\mu - \gamma\langle N \rangle + \beta(y)\langle S \rangle - y,$$

where  $\langle N \rangle$  and  $\langle S \rangle$  are the time-averages of  $S(t)$  and  $N(t)$ . If the invasion fitness  $s_{S,N}(y)$  is negative, then the mutant strain dies out; if  $s_{S,N}(y)$  is positive, then the mutant has a positive probability of invasion.

The environment affects the invasion fitness (3.17) only via the numbers  $\langle N \rangle$  and  $\langle S \rangle$ . Maximum number of resident strategies  $(x_1, \dots, x_k)$  in the given environment follows from the principle of selective neutrality of residents: In this model generically  $k \leq 2$ , meaning that not more than two strategies can coexist. In other words, the set of all  $k$ -tuples  $(x_1, \dots, x_k) \in \mathbb{R}^k$  for which  $\text{Log}(n_1(t)), \dots, \text{Log}(n_k(t))$  are bounded as a function of  $t \geq 0$  has a Lebesgue measure equal to zero for any  $k > 2$ . We therefore need to consider only three cases: disease-free population, monomorphic resident population and dimorphic resident population.

### 3.6.3 Disease-free environment

The dynamics of the disease-free environment is given by

$$(3.18) \quad \begin{aligned} \frac{dS}{dt} &= (\lambda - \mu)S - \gamma NS \\ \frac{dI_i}{dt} &= 0, \end{aligned}$$

where  $N = S$ . The disease-free environment is often called the virgin environment.

If we assume that  $\lambda < \mu$ , then  $S(t) \rightarrow 0$  as  $t \rightarrow \infty$ ; If  $\lambda > \mu$ , then there is a unique and stable positive equilibrium  $(S_0, N_0)$  with  $S_0 = N_0 = \frac{\lambda - \mu}{\gamma}$ . The invasion fitness in the disease-free environment thus is given by

$$(3.19) \quad s_{vir}(y) = -\mu - \gamma N_0 + \beta(y)S_0 - y.$$

The set of strategies  $y$  such that  $s_{vir}(y) > 0$  is called the viability set.

### 3.6.4 Monomorphic environment

In the case of monomorphic population, where one resident strategy  $x$  is present at density  $I$ . The dynamics of the monomorphic environment is given by

$$(3.20) \quad \begin{aligned} \frac{dS}{dt} &= \lambda S - \mu S - \gamma NS - \beta(x)SI \\ \frac{dI}{dt} &= -\mu I - \gamma NI + \beta(x)SI - xI, \end{aligned}$$

where  $N = S + I$ . In the monomorphic environment if  $s_{vir}(x) > 0$  holds, then there is a unique and stable positive equilibrium  $(S_1(x), N_1(x))$  where

$$(3.21) \quad \begin{aligned} S_1(x) &= \frac{(x + \lambda)\gamma + (x + \mu)\beta(x)}{\beta(x)^2} \\ N_1(x) &= \frac{x + \lambda}{\beta(x)}. \end{aligned}$$

The invasion fitness  $s_x(y)$  in the monomorphic environment thus is given by

$$(3.22) \quad s_x(y) = -\mu - \gamma N_1(x) + \beta(y)S_1(x) - y.$$

Which strategy  $y$  can invade depends on the resident strategy  $x$  as shown in the pairwise invadability plot (PIP) below.

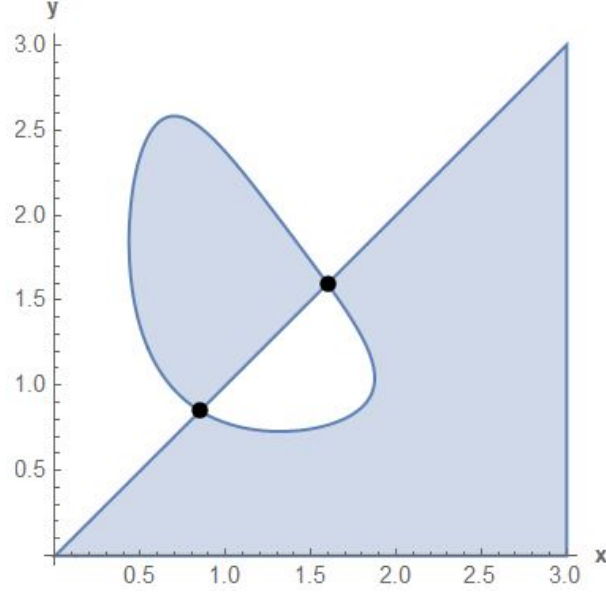


Figure 3.2: The shaded area represents combinations of  $x$  and  $y$  for which the mutant's fitness  $s_x(y)$  is positive. Singularities are presented in the form of two black dots in the figure.

To investigate the possibility of branching points, it is necessary to look at the selection gradient and selection curvature (the second order derivative) of the mutant  $y$  in the monomorphic environment. Selection gradient is thus given by

$$(3.23) \quad \left. \frac{\partial s_e(y)}{\partial y} \right|_{y=x} = \frac{((x + \lambda)\gamma + (x + \mu)\beta(x))\beta'(x)}{\beta(x)^2} - 1,$$

where follows that positive singularities can only exists where  $\beta'(x) > 0$ . Whereas for the selection curvature, which is given by

$$(3.24) \quad \left. \frac{\partial^2 s_e(y)}{\partial y^2} \right|_{y=x} = \frac{((x + \lambda)\gamma + (x + \mu)\beta(x))\beta''(x)}{\beta(x)^2},$$

follows that branching points can only exists where  $\beta''(x) > 0$ .

### 3.6.5 Dimorphic environment

Consider two resident strategies  $x_1$  and  $x_2$  present at densities  $I_1$  and  $I_2$ . Then the corresponding dynamics of the dimorphic environment is given by

$$(3.25) \quad \begin{aligned} \frac{dS}{dt} &= \lambda S - \mu S - \gamma N S - \beta(x_1) S I_1 - \beta(x_2) S I_2 \\ \frac{dI_1}{dt} &= -\mu I_1 - \gamma N I_1 + \beta(x_1) S I_1 - x_1 I_1 \\ \frac{dI_2}{dt} &= -\mu I_2 - \gamma N I_2 + \beta(x_2) S I_2 - x_2 I_2, \end{aligned}$$

where  $N = S + I_1 + I_2$ . Here we can calculate the environment as a function of the resident strategies directly from the invasion fitness, since the invasion fitness of each resident in their own environment is always zero,  $s_{S,N}(x_1) = s_{S,N}(x_2) = 0$  (i.e., selective neutrality of residents). Therefore, we get the following

$$(3.26) \quad \begin{aligned} s_{S,N}(x_1) &= -\mu - \gamma \langle N \rangle + \beta(x_1) \langle S \rangle - x_1 = 0 \\ s_{S,N}(x_2) &= -\mu - \gamma \langle N \rangle + \beta(x_2) \langle S \rangle - x_2 = 0, \end{aligned}$$

from which we solve

$$(3.27) \quad \begin{aligned} \langle S \rangle &= \frac{x_1 - x_2}{\beta(x_1) - \beta(x_2)} \\ \langle N \rangle &= \frac{(\mu + x_1)\beta(x_2) - (\mu + x_2)\beta(x_1)}{\gamma(\beta(x_1) - \beta(x_2))}. \end{aligned}$$

Now the invasion fitness of the mutant  $y$  in a resident population with  $x_1$  and  $x_2$  is

$$(3.28) \quad s_{x_1, x_2}(y) = -\mu - \gamma N_2(x_1, x_2) + \beta(y) S_2(x_1, x_2) - y,$$

where

$$\begin{aligned} S_2(x_1, x_2) &= \frac{x_1 - x_2}{\beta(x_1) - \beta(x_2)} \\ N_2(x_1, x_2) &= \frac{(\mu + x_1)\beta(x_2) - (\mu + x_2)\beta(x_1)}{\gamma(\beta(x_1) - \beta(x_2))}. \end{aligned}$$

The selection gradients of the mutant  $y$  evaluated at the respective resident strategies  $x_1$  and  $x_2$  are given by

$$(3.29) \quad \begin{aligned} \left. \frac{\partial s_{x_1, x_2}(y)}{\partial y} \right|_{y=x_1} &= \frac{(x_1 - x_2)\beta'(x_1)}{\beta(x_1) - \beta(x_2)} - 1 \\ \left. \frac{\partial s_{x_1, x_2}(y)}{\partial y} \right|_{y=x_2} &= \frac{(x_1 - x_2)\beta'(x_2)}{\beta(x_1) - \beta(x_2)} - 1, \end{aligned}$$

which indicate the evolutionary flow in the dimorphic resident population to be as in the figure below.

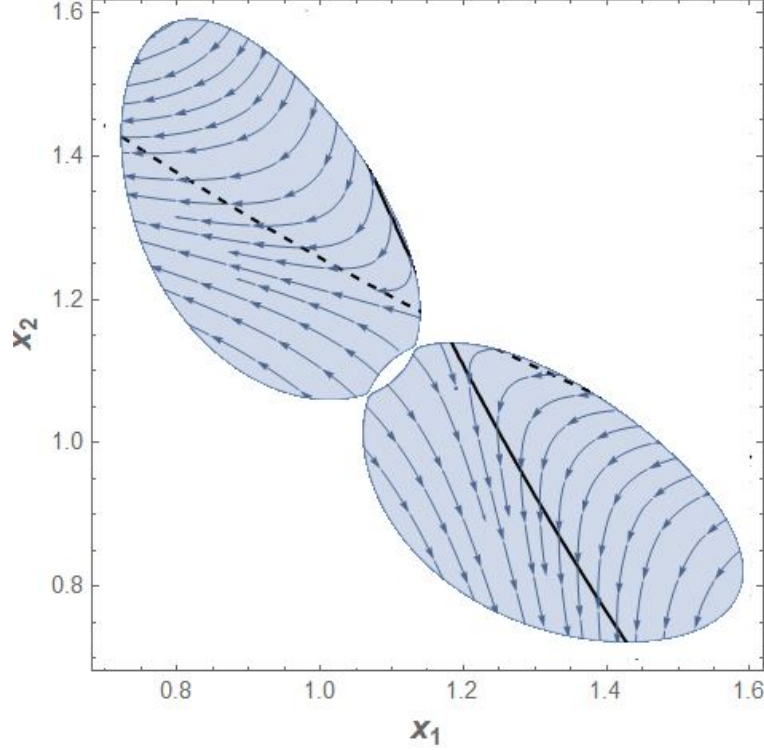


Figure 3.3: Here the shaded area is the region of coexistence. Black line and dashed line are so called evolutionary isoclines, where  $\frac{\partial s_{x_1, x_2}(y)}{\partial y}|_{y=x_1} = 0$  and  $\frac{\partial s_{x_1, x_2}(y)}{\partial y}|_{y=x_2} = 0$  holds. Here we set  $\beta(x) = a + \frac{bx^2}{1+cx^2}$ , where  $a = 3$ ,  $b = 2$  and  $c = 0.244$ . Rest of the parameters are set as  $\lambda = 2.1$ ,  $\mu = 0.1$  and  $\gamma = 1$ .

The symmetry is due to the fact that the  $x_1$  and  $x_2$  are interchangeable. Focusing on the upper-left of the picture, we see that after branching  $x_1$  decreases and  $x_2$  increases until the orbit leaves the blue coexistence region, where  $x_2$  dies out so that the population becomes monomorphic again, but now with a strategy value below the monomorphically repelling singular strategy. So, eventually the strategy (virulence) evolves to zero, where the disease has no longer an effect on the mortality.

# Chapter 4

## Hawk-Dove model with quitting

The generic dynamics of Hawk-Dove game (as in Example 2.0.2) depends on the severity of the injury and the composition of the population. In the population consisting mostly Doves, Hawks will spread, since they are likely to meet only Doves and receive the entire resource  $R$  without any reluctance, while a Dove will only get  $R/2$  when it faces another Dove. But if the population is mostly Hawks, the probability of injuring a contestant is an average half of the battles, and therefore, the gain of for a Hawk is  $(R - C)/2$ , while Doves avoid all combats against Hawks by fleeing.

By including additional rules to the game may results in a game dynamical change, which changes the qualitative properties of evolutionary singularities, changing from repelling to attracting and vice versa. Let me present one example, which to the best of my knowledge, has not been analyzed more than once before by Ollikainen (2018): quitting. Quitting as a strategic decision or mandatory part of the game can be formulated, for example, depending on the payoff alone. If the expected payoff for the player does not actualize after  $N$ -rounds, a player can choose to quit the game. The focus on my model will be on quitting as a mandatory rule of the game.

Quitting, as a strategic decision or mandatory part of the game, leaves the door open for game dynamical abuses if it is not regulated. A player can choose to quit if the opponent plays a strategy that does not result in the wanted payoff, and play against a new opponent, in the hopes of a better payoff. It is reasonable for the player to quit a bad match-up and find a new one if the pairing against an opponent happens immediately after quitting, without any waiting or a penalty. Therefore, it would be wise to add rules to quitting: it should take some fixed amount of rounds or have some probability to find a new opponent if a player chooses to quit. This way, the overall sum of the payoffs after every round decreases if the player is prone to quit. Otherwise, the greedy player would be able to get more favorable match-ups for thysself by trying to face as many opponents with a strategy Dove while playing Hawk strategy itself.

### 4.1 Model description

In this model, the population consists of inactive and active players, where inactive players form the pool, from which each player gets paired with a randomly chosen opponent with

probability  $p \in [0, 1]$ . Active players have already been paired, and are in the game. Let  $x \in [0, 1]$  denote a strategy that occurs in the population as the resident strategy. The strategy  $x$  describes the probability to act as a Hawk in any given round, and respectively to act as a Dove with a probability  $(1 - x)$ . The game dynamics proceed in discrete steps, and we use the notation  $t$  for bookkeeping of time, and players play games in rounds from  $1, 2, 3, \dots$ , getting the payoff at the end of every round. Payoffs are defined as in prisoner's dilemma: *Suckers payoff* for Dove against Hawk, *Punishment* for Hawk against Hawk, *Reward* for Dove against Dove, and *Temptation* for Hawk against Dove. The *Reward* ( $R$ ) can be considered always bigger, than the *Punishment* ( $P$ ) because the resource is shared in the case of *Reward*, whereas in the case of *Punishment* the resource is obtained entirely by the player who wins the fight but with the cost of injury. Without loss of generality, we can assume that the payoff *Temptation* is 1, which represents the highest payoff available, and other payoffs are some proportions of this. We can assume that withdrawal is a cost-less action. Therefore, *Suckers payoff* is 0. For payoffs *Reward* and *Punishment*, we assume that  $R \in [\frac{1}{2}, 1)$  and  $P \in (-\frac{1}{2}, \frac{1}{2})$ .

**The quitting rule:** A player quits and terminates the game if its opponent acts as a Hawk, they are returned back to the pool as inactive players. Otherwise, if both act as a Dove, both players proceed to the ongoing rounds as active players.

The notations in the game dynamics equations are defined as following: the proportions of players on round  $i$  are represented as  $q^i(t, x)$ , where  $i = 0, 1, 2, \dots$ . Case  $i = 0$  corresponds to inactive players in the pool denoted by  $q^0(t, x)$ . Time  $t$  in this model is discrete, and it gets values from  $t \in \mathbb{N}_+$ .

Game dynamics equations for the population with resident strategy  $x$  are:

$$\begin{cases} q^0(t+1, x) &= -pq^0(t, x) + \sum_{n=1}^{\infty} q^n(t, x) \overbrace{(x(1-x) + (1-x)x + x^2)}^{\text{Probability that player acts as a Hawk}} \\ q^1(t+1, x) &= pq^0(t, x) - q^1(t, x) \\ q^2(t+1, x) &= q^1(t, x)(1-x)^2 - q^2(t, x) \\ &\vdots \\ q^j(t+1, x) &= q^{j-1}(t, x)(1-x)^2 - q^j(t, x), \quad j = 2, 3, \dots \end{cases}$$

The following notion is taken into account on every round-state: how many players are coming in either from the pool or from another round, and how many players are leaving the current round. The game rule states that only those players who play Dove and face other Doves, advance further in a the same game without returning to the pool. Every other player either faced an opponent playing a Hawk or played itself, and therefore, their game terminates and they are returned to the pool.

For convenience, I drop the time  $t$  from the notations since the analysis of this model is done at equilibrium solutions. In other words, an equilibrium is a game dynamic state that does not change with time. At the equilibrium, the game dynamics equations can be solved, starting from the second equation, as follows:

$$\hat{q}^1(x) = p\hat{q}^0(x) - \hat{q}^1(x) \Leftrightarrow \hat{q}^1(x) = \frac{1}{2}p\hat{q}^0(x),$$

and the same reasoning holds for the third equation

$$\hat{q}^2(x) = \hat{q}^1(x)(1-x)^2 - \hat{q}^2(x) \Leftrightarrow \hat{q}^2(x) = \frac{1}{4}p\hat{q}^0(x)(1-x)^2,$$

and the logic can be iterated to all consecutive rounds. Hence, the equilibrium equations for the resident strategy  $x$  are given by

$$\begin{cases} \hat{q}^1(x) &= \frac{1}{2}p\hat{q}^0(x) \\ \hat{q}^2(x) &= \frac{1}{4}p\hat{q}^0(x)(1-x)^2 \\ \hat{q}^3(x) &= \frac{1}{8}p\hat{q}^0(x)(1-x)^4 \\ &\vdots \\ \hat{q}^j(x) &= 2^{-j}p\hat{q}^0(x)(1-x)^{2(j-1)}, \quad j = 1, 2, \dots \end{cases}$$

By definition  $\sum_{n=0}^{\infty} \hat{q}^n(x) = 1$ . Therefore, the variable  $\hat{q}^0(x)$  is given by

$$(4.1) \quad \begin{aligned} \hat{q}^0(x) &= 1 - \sum_{n=1}^{\infty} \hat{q}^n(x) = 1 - p\hat{q}^0(x) \sum_{n=1}^{\infty} 2^{-n}(1-x)^{2(n-1)} \Leftrightarrow \\ \hat{q}^0(x) &= \frac{1}{1 + p \sum_{n=1}^{\infty} 2^{-n}(1-x)^{2(n-1)}} = \frac{1}{1 + p(\frac{1}{1-(x-2)x})} = \frac{1 - (x-2)x}{1 - (x-2)x + p}. \end{aligned}$$

This function acts as a pool argument, which contains all inactive players.

Assume an initially rare mutant strategy  $y = x + \sigma$ , for small  $\sigma$ , taking into account that  $y \in [0, 1]$ . Therefore, in the overall population the mutant strategy  $y$  plays against the resident strategy  $x$  every time, and it is safe to assume that the mutant is so rare in the population that it never plays against itself. Simultaneously, the resident strategy  $x$  mostly plays against other residents in the population, facing extremely rarely the mutant strategy  $y$ . The corresponding game dynamics equations for the population of rare mutant strategy  $y$  are:

$$\begin{cases} \begin{array}{l} q^0(t+1, y) = -pq^0(t, y) + \sum_{n=1}^{\infty} q^n(t, y) \overbrace{(y(1-x) + (1-y)x + yx)}^{\text{Probability that player acts as a Hawk}} \\ q^1(t+1, y) = pq^0(t, y) - q^1(t, y) \\ q^2(t+1, y) = q^1(t, y)(1-x)(1-y) - q^2(t, y) \\ \vdots \\ q^j(t+1, y) = q^{j-1}(t, y)(1-x)(1-y) - q^j(t, y), \quad j = 2, 3, \dots \end{array} \end{cases}$$

and the corresponding game dynamics equations at the equilibrium are given by

$$\begin{cases} \hat{q}^1(y) &= \frac{1}{2}p\hat{q}^0(y) \\ \hat{q}^2(y) &= \frac{1}{4}p\hat{q}^0(y)(1-x)(1-y) \\ \hat{q}^3(y) &= \frac{1}{8}p\hat{q}^0(y)((1-x)(1-y))^2 \\ &\vdots \\ \hat{q}^j(y) &= 2^{-j}p\hat{q}^0(y)((1-x)(1-y))^{j-1}, \quad j = 1, 2, \dots \end{cases}$$



The only visible difference between the equations for the mutant strategy  $y$  and the resident strategy  $x$  is  $(1 - y)$  representing the proportion of time that mutant  $y$  acts as a Dove within the mutant population. The variable  $\hat{q}(y)$  for the mutant is given by

$$(4.2) \quad \begin{aligned} \hat{q}^0(y) &= 1 - \sum_{n=1}^{\infty} \hat{q}^n(y) = 1 - p\hat{q}^0(y) \sum_{n=1}^{\infty} 2^{-n}((1-x)(1-y))^{n-1} \quad \Leftrightarrow \\ \hat{q}^0(y) &= \frac{1}{1 + p \sum_{n=1}^{\infty} 2^{-n}((1-x)(1-y))^{n-1}} = \frac{1}{1 + p(\frac{1}{1+x+y-xy})} = \frac{1+x+y-xy}{1+x+y-xy+p}. \end{aligned}$$

## 4.2 Invasion fitness and properties of singular strategy

The resident strategy  $x$  determines whether a rare mutant strategy  $y$  can have a positive probability of an invasion. The interesting question here is: What happens in the long-term of repeated successful invasion events? To answer this, I will give two definitions and lemmas. First, the payoff functions for both resident  $x$  and mutant  $y$  players are defined as

**Definition 4.2.1.** Long-term expected payoff per round for a player playing strategy  $x$  against a population of strategy  $x$  players the payoff function is:

$$\begin{aligned} E(x, x) &= 0 \cdot \hat{q}^0(x) + (1 - \hat{q}^0(x))(x(1-x) \cdot 1 + (1-x)^2 R + (1-x)xP + x^2 \cdot 0) \\ &= (1 - \hat{q}^0(x))(\underbrace{x(1-x)}_{\text{Temptation}} + \underbrace{(1-x)^2 R}_{\text{Reward}} + \underbrace{(1-x)xP}_{\text{Punishment}} + \underbrace{x^2 \cdot 0}_{\text{Sucker's payoff}}), \end{aligned}$$

and for a player playing the mutant strategy  $y$  against a population with strategy  $x$  is:

$$\begin{aligned} E(y, x) &= 0 \cdot \hat{q}^0(y) + (1 - \hat{q}^0(y))(y(1-x)T + (1-y)(1-x)R + (1-y)xP + yxS) \\ &= (1 - \hat{q}^0(y))(\underbrace{y(1-x)}_{\text{Temptation}} + \underbrace{(1-y)(1-x)R}_{\text{Reward}} + \underbrace{(1-y)xP}_{\text{Punishment}} + \underbrace{yxS}_{\text{Sucker's payoff}}). \end{aligned}$$

Here terms  $0 \cdot \hat{q}^0(x)$  and  $0 \cdot \hat{q}^0(y)$  represents players in the pool, where they cannot gain anything and act as inactive players of the game.

The invasion fitness of a mutant is defined as its net benefit when compared to the mean payoff to the resident.

**Definition 4.2.2.** The invasion fitness is represented in the form of payoff functions:

$$(4.3) \quad s_x(y) = E(y, x) - E(x, x),$$

where the lower index  $x$  represents the resident strategy  $x$ .

Depending on the sign of this function, it will decide the possibility of an invasion of a mutant strategy  $y$ . If the sign is positive, the mutants can invade the resident population with a positive probability. Otherwise, the resident population will be unaffected by the mutant strategy individuals, and mutants will die out with the probability of one. The population then will evolve in the direction described by the fitness gradient as defined in (3.7). The fitness gradient in this model is given by

$$(4.4) \quad \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x} = \frac{p(1+p-2R-pR+(P+2R+p(P+R-1))x+(P-1)x^2)}{(1+p-(-2+x)x)^2},$$

which is the evolutionarily singular strategy  $x^*$  when the selection gradient is zero. In other words, when  $\frac{\partial s_x(y)}{\partial y}|_{y=x=x^*} = 0$  holds. By solving roots of the fitness gradient (4.4) results in two values:

$$(4.5) \quad \begin{aligned} x_1^* &= \frac{P + 2R + p(P + R - 1) - \sqrt{4(P - 1)(p(R - 1) + 2R - 1) + (P + 2R + p(P + R - 1))^2}}{2(1 - P)} \\ x_2^* &= \frac{P + 2R + p(P + R - 1) + \sqrt{4(P - 1)(p(R - 1) + 2R - 1) + (P + 2R + p(P + R - 1))^2}}{2(1 - P)}. \end{aligned}$$

These values correspond to evolutionarily singular strategies, if and only if, they are real valued and  $0 \leq x_1^*, x_2^* \leq 1$ . Next, I will present two lemmas concerning the qualitative properties and the existence of the singular strategies. In the strategy-interval  $[0, 1]$  there exists at most two singular strategies simultaneously, and they can be either evolutionarily repelling or attracting evolutionary trajectories near them. By continuity of the fitness gradient (4.4), it can change the sign only at the singular strategy points  $x_1^*$  and  $x_2^*$ . Therefore, the qualitative properties of the singular strategies can be deduced from the values of the fitness gradient (4.4) at the boundary strategies  $x^* = 0$  and  $x^* = 1$ .

**Lemma 4.2.1.** Let  $p \in [0, 1]$  and denote  $R^* = \frac{1+p}{2+p}$ . Suppose that  $P \in (0, \frac{1}{2})$  and  $R \in [\frac{1}{2}, 1)$ . Then:

- (a) The boundary strategies  $x^* = 0$  and  $x^* = 1$  are local evolutionary attractors for  $R > R^*$ . The basins of attraction are separated by a unique evolutionarily repelling singular strategy  $x^* \in (0, 1)$
- (b) The boundary strategy  $x^* = 1$  is a global evolutionary attractor for  $R \leq R^*$ .

*Proof.* I will prove all the statements in the order they are presented in the lemma. First, I show that for  $P \in (0, \frac{1}{2})$ , the roots of the fitness gradient (4.5) are strictly positive and real valued. The discriminant in the square root of (4.5) is given by

$$(4.6) \quad \begin{aligned} \text{Disc}_1 &:= 4(P - 1)(p(-1 + R) + 2R - 1) + (P + 2R + p(P + R - 1))^2 \\ &= (-2 + p(-1 + P) + P)^2 + 2(2 + p)(-2 + p(-1 + P) + 3P)R + (2 + p)^2 R^2, \end{aligned}$$

which is an parabola in terms of  $R$  that opens up, and has the minimum at

$$(4.7) \quad R_{\min} = \frac{-2(2 + p)(-2 + p(-1 + P) + 3P)}{2(2 + p)^2}.$$

By replacing  $R$  with  $R_{\min}$  in the equation (4.6), it follows

$$\text{Disc}_1(R_{\min}) = -4(2 + p)(P - 1)P,$$

which is strictly positive for all  $p \in [0, 1]$  and  $P \in (0, \frac{1}{2})$ . Therefore, both roots in (4.5) of the fitness gradient (4.4) are real valued. From observing the (4.5) it clearly follows that  $x_1^*$  and  $x_2^*$  are positive.

Next, I will show that the root  $x_2^*$  is not in the interval  $[0, 1]$ , and hence, it is never a proper singular strategy. It is sufficient to show that the following holds

$$x_2^* = \frac{P + 2R + p(P + R - 1) + \sqrt{4(P - 1)(p(R - 1) + 2R - 1) + (P + 2R + p(P + R - 1))^2}}{2(1 - P)} > 1$$

$$\Leftrightarrow \sqrt{4(P - 1)(p(-1 + R) + 2R - 1) + (P + 2R + p(P + R - 1))^2} > p + P - pP - 2 + (-2 - p)R.$$

Suppose  $p + P - pP - 2 + (-2 - p)R > 0$ , otherwise the above statement is always true. Then, by taking the square of both sides, it follows

$$(4(P - 1)(p(R - 1) + 2R - 1) + (P + 2R + p(P + R - 1))^2) > (p + P - pP - 2 + (-2 - p)R)^2$$

$$\Leftrightarrow (2 + p)(-1 + P)P < 0,$$

which holds for every  $p$  and  $P$ . Therefore, the root satisfies  $x_2^* > 1$  for all  $R$ , and hence, it is never a singularity.

Now set  $R = R^* + \epsilon$ , where  $0 < \epsilon < 1 - \frac{1+p}{2+p}$ . Observe that at the boundaries of the strategy-interval  $[0, 1]$ , the fitness gradient has the following values:

$$(4.8) \quad \frac{\partial s_x(y)}{\partial y} \Big|_{y=x=0} = -\frac{p(2+P)\epsilon}{(1+p)^2} < 0,$$

$$\frac{\partial s_x(y)}{\partial y} \Big|_{y=x=1} = \frac{pP}{2+p} > 0,$$

for all  $P \in (0, \frac{1}{2})$  and  $p \in (0, 1)$ , from which it is clear that both of these boundary values are local evolutionary attractors.

Next, I will show that  $x_1^*$  is the unique and evolutionary repelling singular strategy in the interval  $[0, 1]$ . It is sufficient to show that  $x_1^* < 1$  holds for every  $p \in [0, 1]$  and  $P \in (0, \frac{1}{2})$  that is,

$$x_1^* = \frac{1 + P + pP + 2\epsilon + p\epsilon - \sqrt{4(2+p)(P-1)\epsilon + (1 + P + pP + 2\epsilon + p\epsilon)^2}}{2(1 - P)} < 1$$

$$\Leftrightarrow \sqrt{4(2+p)(P-1)\epsilon + (1 + P + pP + (2+p)\epsilon)^2} > -1 + (3+p)P + \epsilon(2+p).$$

Suppose  $-1 + (3+p)P + \epsilon(2+p) > 0$ , otherwise, the statement above is always true. Then, by taking the square of both sides, it follows

$$4(2+p)(P-1)\epsilon + (1 + P + pP + (2+p)\epsilon)^2 > (-1 + (3+p)P + \epsilon(2+p))^2$$

$$\Leftrightarrow (2+p)(-1 + P)P < 0,$$

which holds for every  $p$  and  $P$ . Therefore, the singular strategy  $x_2^* \in (0, 1)$  is the unique singularity for  $R > R^*$ . By the continuity of the fitness gradient (4.4), it changes the sign only at the singularity  $x_1^*$ . Thus, by (4.8) the fitness gradient is negative for all  $x < x_1^*$ , and positive for all  $x > x_1^*$ . Therefore, the direction of the evolution is always towards boundary strategies  $x = 0$  and  $x = 1$ , making the singularity  $x_1^*$  repelling.

Lastly, suppose that  $R = R^* - \epsilon$ , where  $0 \leq \epsilon < \frac{p}{2(2+p)}$ . Then, the fitness gradient as in (4.4) is given by

$$(4.9) \quad \frac{\partial s_x(y)}{\partial y} \Big|_{y=x} = \frac{px(1-x + P(1+p+x)) - p(2+p)(-1+x)\epsilon}{(1+p - (-2+x)x)^2},$$

which is positive for all  $x \in [0, 1]$ , and hence  $x = 1$  is the global evolutionary attractor. Therefore, there are no singularities for  $R \leq R^*$ . This concludes the proof.  $\square$

**Lemma 4.2.2.** Let  $p \in [0, 1]$  and denote  $R^* = \frac{1+p}{2+p}$ . Suppose that  $P \in (-\frac{1}{2}, 0)$  and  $R \in [\frac{1}{2}, 1)$ . Then for every  $p$  there exists an interval  $\omega = (R^*, R^* + \delta)$ , where  $\delta > 0$  that satisfies:

- (a) If  $R \in \omega$ , there exists two singularities  $x_1^*$  and  $x_2^*$ , where  $x_1^* < x_2^*$ , such that  $x_2^*$  and the boundary strategy  $x^* = 0$  are local evolutionary attractors. The singularity  $x_1^*$  is evolutionarily repelling that separates the basins of attraction.
- (b) If  $R \geq R^* + \delta$ , then the boundary strategy  $x^* = 0$  is the global evolutionary attractor.
- (c) If  $R \leq R^*$ , then there exists a unique singularity  $x^* \in (0, 1)$  that is the global evolutionary attractor.

*Proof.* I will prove all the statements in the order they are presented in the lemma. First, I will define the interval  $\omega$  and  $\delta$ . Let  $R = \frac{1+p}{2+p} + \epsilon$ , where  $0 < \epsilon < 1 - \frac{1+p}{2+p}$ . The roots of the fitness gradient (4.5) are then given by

$$(4.10) \quad \begin{aligned} x_1^* &= \frac{1 + (1+p)P + (2+p)\epsilon - \sqrt{(1+P+pP)^2 + 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2}}{2(1-P)} \\ x_2^* &= \frac{1 + (1+p)P + (2+p)\epsilon + \sqrt{(1+P+pP)^2 + 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2}}{2(1-P)}. \end{aligned}$$

Next, I examine when the discriminant of the above equations are positive for  $P \in (-\frac{1}{2}, 0)$ . The discriminant is given by

$$(4.11) \quad \text{Disc}_2 := (1+P+pP)^2 + 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2,$$

which is positive when the following holds

$$\begin{aligned} \text{Disc}_2 &= (1+P+pP)^2 + 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2 > 0 \\ \Leftrightarrow &\frac{(1+P+pP)^2 + 2\epsilon(2+p)(-1+(3+p)P)}{(2+p)^2} + \epsilon^2 > 0 \\ \Leftrightarrow &\frac{2\epsilon(-1+(3+p)P)}{(2+p)} + \epsilon^2 > \frac{-(1+P+pP)^2}{(2+p)^2} \\ \Leftrightarrow &\frac{(-1+(3+p)P)^2}{(2+p)^2} + \frac{2\epsilon(-1+(3+p)P)}{(2+p)} + \epsilon^2 > \frac{-(1+P+pP)^2}{(2+p)^2} + \frac{(-1+(3+p)P)^2}{(2+p)^2} \\ \Leftrightarrow &\left(\frac{-1+(3+p)P}{2+p} + \epsilon\right)^2 > \frac{-(1+P+pP)^2}{(2+p)^2} + \frac{(-1+(3+p)P)^2}{(2+p)^2}. \end{aligned}$$

Note that  $\frac{-1+(3+p)P}{2+p} + \epsilon < 0$  for all  $0 < \epsilon < \frac{1}{2+p}$ ,  $p \in (0, 1)$  and  $P \in (-\frac{1}{2}, 0)$ . From this observation, it follows that

$$(4.12) \quad \begin{aligned} \epsilon &< -\sqrt{\frac{-(1+P+pP)^2}{(2+p)^2} + \frac{(-1+(3+p)P)^2}{(2+p)^2}} - \frac{-1+(3+p)P}{2+p} \\ \Leftrightarrow \quad \epsilon &< -2\sqrt{\frac{(-1+P)P}{2+p} + \frac{1-(3+p)P}{2+p}}. \end{aligned}$$

Choose now  $\delta = -2\sqrt{\frac{(-1+P)P}{2+p} + \frac{1-(3+p)P}{2+p}}$ . Then the discriminant (4.11) is positive in the interval  $\omega = (R^*, R^* + \delta)$ .

Now assume that  $\epsilon < \delta$ , so that  $R = \frac{1+p}{2+p} + \epsilon \in \omega$ . Next, I will show that both roots of the fitness gradient  $x_1^*$  and  $x_2^*$  belong in the interval  $[0, 1]$ . First, I show the conditions for  $0 < x_1^*$ . The singular strategy being positive is equivalent with

$$\begin{aligned} 1 + (1+p)P + (2+p)\epsilon - \sqrt{(1+P+pP)^2 + 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2} &> 0 \\ \Leftrightarrow (1 + (1+p)P + (2+p)\epsilon)^2 - (1+P+pP)^2 + 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2 &> 0 \\ &\Leftrightarrow -4(2+p)(-1+P)\epsilon > 0, \end{aligned}$$

which holds for all  $p, P$  and  $\epsilon$ . Next, I show that  $x_1^* < 1$ , which is equivalent with the condition

$$\begin{aligned} \frac{1 + (1+p)P + (2+p)\epsilon - \sqrt{(1+P+pP)^2 + 2\epsilon(2+p)((3+p)P - 1) + (2+p)^2\epsilon^2}}{2(1-P)} &< 1 \\ \Leftrightarrow ((3+p)P - 1) + (2+p)\epsilon &< \sqrt{(1+P+pP)^2 + 2\epsilon(2+p)((3+p)P - 1) + (2+p)^2\epsilon^2}, \end{aligned}$$

which holds for all  $p, P$  and  $\epsilon$ , because the left-hand side of the above inequality is always negative as long as (4.12) holds. Therefore,  $x_1^*$  is a singular strategy as  $x_1^* \in (0, 1)$ .

Similarly, for the singular strategy  $x_2^*$ , I will first show the conditions when it is positive. The square root part of  $x_2^*$  is positive as well as the denominator. It is sufficient to show that

$$\begin{aligned} 1 + (1+p)P + (2+p)\epsilon &> 0 \\ \Leftrightarrow \quad \frac{-(1+p)P - 1}{2+p} &< \epsilon, \end{aligned}$$

where the left-hand side of the latter inequality is always negative when  $P \in (-\frac{1}{2}, 0)$  and  $p \in [0, 1]$ . Therefore, the singular strategy  $x_2^*$  is positive with all  $p, P$  and  $\epsilon$ . Next, I show that  $x_2^* < 1$ , which is equivalent with the condition

$$\begin{aligned} \frac{1 + (1+p)P + (2+p)\epsilon + \sqrt{(1+P+pP)^2 + 2\epsilon(2+p)((3+p)P - 1) + (2+p)^2\epsilon^2}}{2(1-P)} &< 1 \\ \Leftrightarrow \sqrt{(1+P+pP)^2 + 2\epsilon(2+p)((3+p)P - 1) + (2+p)^2\epsilon^2} &< (1 - (3+p)P) + (-2-p)\epsilon \\ \Leftrightarrow (1+P+pP)^2 + 2\epsilon(2+p)((3+p)P - 1) + (2+p)^2\epsilon^2 - ((1 - (3+p)P) + (-2-p)\epsilon)^2 &< 0 \\ \Leftrightarrow -4(2+p)(-1+P)P &< 0, \end{aligned}$$

which holds for all  $p$  and  $P \in (-\frac{1}{2}, 0)$ . By taking the square of both sides in the above equation, the inequality holds as long as (4.12) holds.

The qualitative properties, repelling or attracting, of the singular strategies  $x_1^*$  and  $x_2^*$  can be deduced from observing the fitness gradient at the boundary strategies  $x^* = 0$  and  $x^* = 1$  when  $R = \frac{1+p}{2+p} + \epsilon$ . Similarly as in (4.8) the fitness gradient has the following values:

$$(4.13) \quad \begin{aligned} \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x=0} &= -\frac{p(2+P)\epsilon}{(1+p)^2} < 0, \\ \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x=1} &= \frac{pP}{2+p} < 0, \end{aligned}$$

for all  $P \in (-\frac{1}{2}, 0)$  and  $p \in (0, 1)$ , from which it is clear that boundary strategy  $x^* = 0$  is attracting evolutionary trajectories towards it and the other boundary strategy  $x^* = 1$  is repelling evolutionary trajectories away from it. From this notion and by the continuity of the fitness gradient (4.4), it can only change the sign at the singular strategies  $x_1^*$  and  $x_2^*$ . Thus, by (4.13) the fitness gradient is negative for all  $x < x_1^*$  and positive for all  $x_1^* < x < x_2^*$  and again negative for all  $x_2^* < x$ . Therefore, the direction of the evolution is either towards boundary strategy  $x^* = 0$  or the singular strategy  $x_2^*$  as they are attracting solution near them. The basins of these attractors are separated by the singular strategy  $x_1^*$ , which is evolutionarily repelling evolutionary trajectories. This concludes the first statement of this lemma.

For the second statement, let  $R = \frac{1+p}{2+p} + \epsilon$ , where  $0 < \delta < \epsilon$ . Then the roots of the fitness gradient (4.10) are not real valued anymore by the notion of (4.11) and (4.12). Thus, singular strategies  $x_1^*$  and  $x_2^*$  do not result in real value solutions, and therefore, the behavior is defined by boundary strategies  $x^* = 0$  and  $x^* = 1$  completely. From (4.13) it is clear that the direction of the evolution is always towards boundary strategy  $x^* = 0$ . Therefore, the boundary strategy  $x^* = 0$  is a global evolutionary attractor. This concludes the second statement.

Lastly, let  $R = \frac{1+p}{2+p} - \epsilon$ , where  $0 < \epsilon < \frac{1+p}{2+p} - \frac{1}{2}$ . The roots of the fitness gradient (4.5) are then given by

$$(4.14) \quad \begin{aligned} x_1^* &= \frac{1 + (1+p)P - (2+p)\epsilon - \sqrt{(1+P+pP)^2 - 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2}}{2(1-P)} \\ x_2^* &= \frac{1 + (1+p)P - (2+p)\epsilon + \sqrt{(1+P+pP)^2 - 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2}}{2(1-P)}. \end{aligned}$$

Here the discriminant is always positive as long as  $p \in (0, 1)$ ,  $P \in (-\frac{1}{2}, 0)$  and  $0 < \epsilon < \frac{1+p}{2+p} - \frac{1}{2}$  holds. Next, I will show that the root  $x_1^*$  is not inside the interval  $[0, 1]$ , whereas the root  $x_2^*$  is in the interval  $[0, 1]$ . Note that the following inequality holds for the roots

$$(4.15) \quad \begin{aligned} \sqrt{(1+P+pP)^2 - 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2} &> 1 + (1+p)P - (2+p) \\ \Leftrightarrow (1+P+pP)^2 - 2\epsilon(2+p)(-1+(3+p)P) + (2+p)^2\epsilon^2 - (1 + (1+p)P - (2+p))^2 &> 0 \\ \Leftrightarrow -4((2+p)(-1+P))\epsilon &> 0, \end{aligned}$$

for all  $p, P$  and  $\epsilon$ . Therefore, the root  $x_1^* \notin [0, 1]$ . Lets examine whether the root  $x_2^*$  is inside the interval  $[0, 1]$ . The inequality (4.15) guarantees that the root  $x_2^* > 0$ . It is sufficient to check whether  $x_2^* < 1$  holds:

$$\begin{aligned}
& \frac{1 + (1 + p)P - (2 + p)\epsilon + \sqrt{(1 + P + pP)^2 - 2\epsilon(2 + p)(-1 + (3 + p)P) + (2 + p)^2\epsilon^2}}{2(1 - P)} < 1 \\
& \Leftrightarrow \sqrt{(1 + P + pP)^2 - 2\epsilon(2 + p)(-1 + (3 + p)P) + (2 + p)^2\epsilon^2} < (1 - (3 + p)P) + (2 + p)\epsilon \\
& \Leftrightarrow (1 + P + pP)^2 - 2\epsilon(2 + p)(-1 + (3 + p)P) + (2 + p)^2\epsilon^2 - ((1 - (3 + p)P) + (2 + p)\epsilon)^2 > 0 \\
& \Leftrightarrow -4(2 + p)(-1 + P)P > 0,
\end{aligned}$$

which holds for all  $p$  and  $P$ . Therefore,  $x_2^*$  is a singular strategy as it satisfies  $x_2^* \in (0, 1)$ . Whether it is evolutionarily repelling or evolutionary attractor that is given by the behavior of the fitness gradient (4.4) at the boundary strategies  $x^* = 0$  and  $x^* = 1$ . With the value  $R = \frac{1+p}{2+p} - \epsilon$  the fitness gradient is same as in (4.9), and it gets the following values at the boundaries

$$\begin{aligned}
(4.16) \quad & \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x=0} = \frac{p(2+p)\epsilon}{(1+p)^2} > 0, \\
& \left. \frac{\partial s_x(y)}{\partial y} \right|_{y=x=1} = \frac{pP}{2+p} < 0,
\end{aligned}$$

for all  $P \in (-\frac{1}{2}, 0)$  and  $p \in (0, 1)$ , from which it is clear that the both of the boundary strategies are repelling evolutionary trajectories away from them. Hence, the fitness gradient is positive for all  $x < x_2^*$  and negative for all  $x_2^* < x$ . Thus, the direction of the evolution is towards the singular strategy  $x_2^*$ . Therefore, the singular strategy  $x_2^*$  is the unique global evolutionary attractor. This concludes the proof  $\square$

Adding the quitting rule as a mandatory part of the iterated Hawk-Dove game allows strategies such as all-Dove and mixed-strategy profiles that are not considered as worthwhile strategies in the standard iterated Hawk-Dove game to be worthwhile. This claim is supported by the lemmas presented above, which explain the behavior of each strategy in the game dynamics environment.

Lastly, I present few figures which illustrates the cases discussed in both lemmas 4.2.1 and 4.2.2.

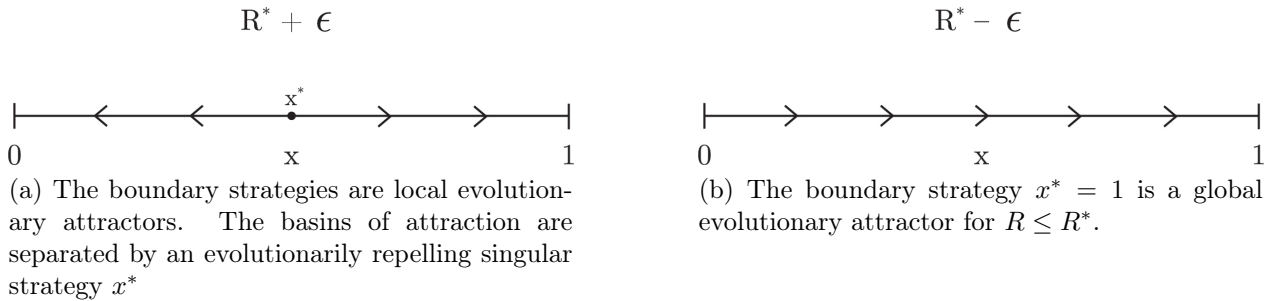


Figure 4.1: Lemma 4.2.1 cases

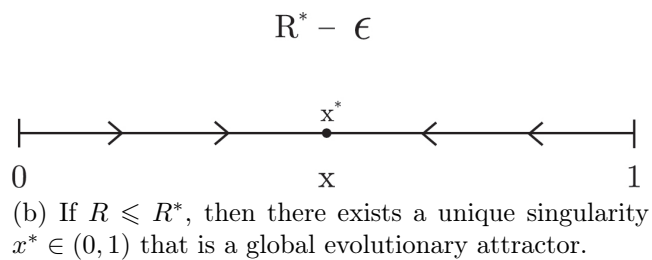
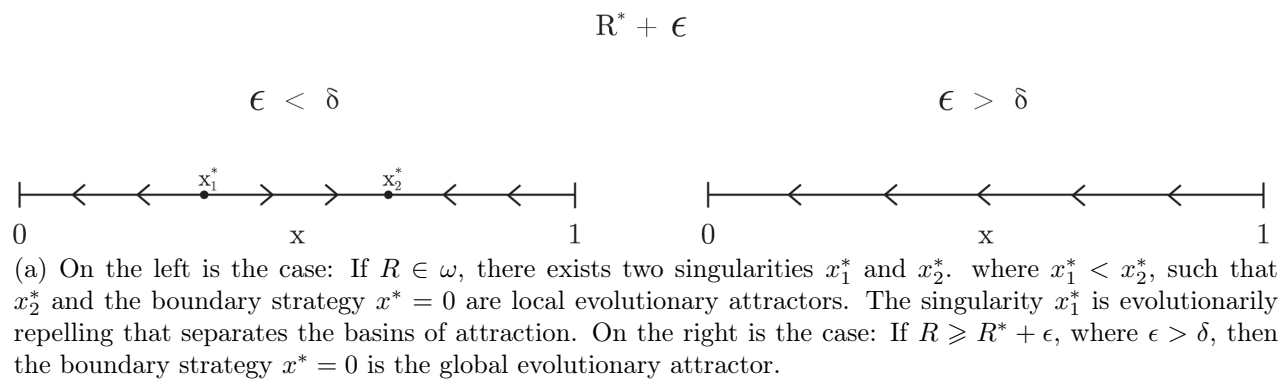


Figure 4.2: Lemma 4.2.2 cases



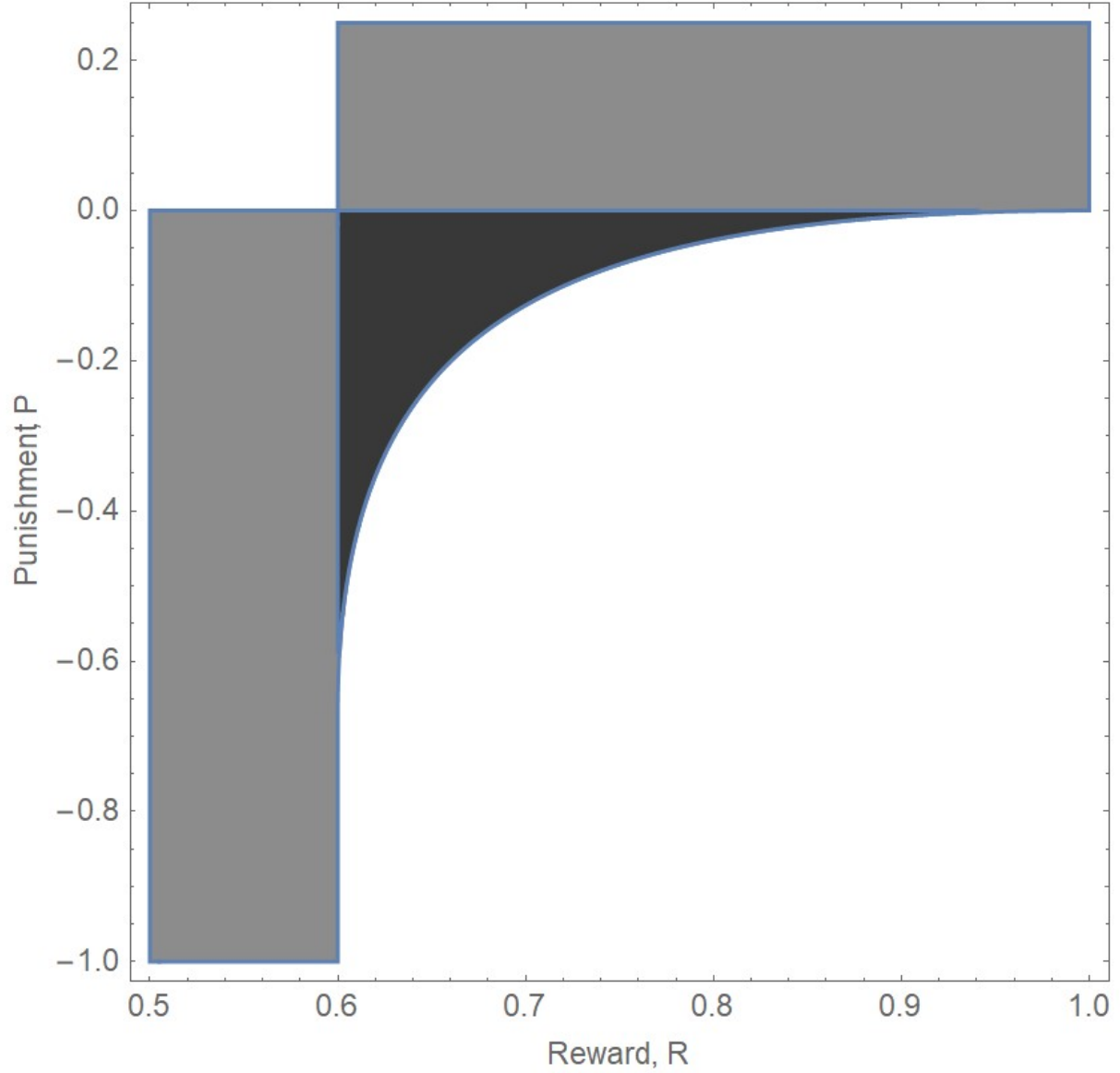


Figure 4.3: This is the combined picture of the information on both lemmas. In the light gray areas exists at most one singular strategy, whereas in the darker gray area exist two singular strategies. Blank spaces represent no singular strategies. In this figure the probability  $p$  is fixed to be  $p = \frac{1}{2}$ .

# Chapter 5

## Discussion

The notion of quitting as a mandatory rule for the players, and the introduction of the pool, create an interesting twist for a rather simple Hawk-Dove game. Typically the Hawk-Dove game goes one of the following ways: If the cost of injury is lower than possible gain, then Hawks are evolutionarily stable strategy. In the vice versa situation, Doves become a more preferred option over injured Hawks. What I showed in this model is when you add one realistic possibility, quitting, for the individual as a mandatory rule, it changes the dynamics and creates an evolutionarily stable mixed strategy equilibrium. Adding quitting requires to introduce the pool mechanic into the game, which could be modified further to utilize more versatile game dynamics. Opting to quit can be argued as a rational option for the individual to choose, and it does exist in one way or another. Retreating away from a threatening situation or stop playing a game, which does not result in payoff, seems to be the more rational move for any individual to choose. In general, this model represents an analysis with pre-existing and well-defined tools but with new assumptions taken into account, which successively leads up to results as evolutionarily stable equilibrium.

The model itself is neither perfect nor complete at this moment, and there exist many weaknesses in it. The group of conditions set by the game rule and the form of the game dynamics results in a variety of equilibria, which are attainable only in certain circumstances. Letting the payoffs *Reward*  $R$  and *Punishment*  $P$  to roam in a more broad interval will ensue more attracting and repelling equilibria with more strict rules, which in turn, represents more diverse game dynamics.

Most of the assumptions made in this model are similar to the regular Hawk-Dove game or the Prisoner's dilemma. The existence of the pool and the mandatory rule to quit makes all the difference, compared to those two models. The quitting keeps the stream of players constant toward the pool from the game, where the probability  $p$  regulates the number of players let to take part in the game. Those two notions together create an interesting dynamic between the pool population and players in the game. When playing a more aggressive strategy, presumably Hawk, a player, spends on average, more time in the pool than a non-aggressive strategy. The reason for this is simple, quitting after a player faced a Hawk strategy puts both players back in the pool, compared to the Dove strategy, where both can keep on playing until the game ends (until the  $N$ :th round is reached). The balance between aggressive and cooperative strategies are both dependent on probability  $p$ , which in turn makes the game interesting if this model is analyzed even further.

The pool does not reach its full potential in this model. Neither punishment for quitting early nor entrance fee to take part in the game do not exist in this model. Pool could have a more defining role; if a player quits after the current round and goes back to the pool, then the player needs to wait for one to two rounds until rejoining is possible. An entrance fee could be another restriction to spice up the game or paying some amount of the resource to raise the possibility to pair on the next round.

This model was only a scratch of the surface, barely showing more than the essential traits, here I mean the pool and the possibility to quit. A more interesting question here is: what comes after this model? Can this be expanded further or generalized in any way? I looked onto multiple questions during the thesis that I was not able to answer outright. I will name a few examples of how to expand this current model into a more complicated one.

Consider a case where players have a memory of two to five rounds or even more. The quitting could be implemented if every player has some payoff threshold that they demand the memory interval, which is counted in the form of rounds. If the threshold cannot be attained, a player would quit the game and move to the pool. One example could be for working labor in the form of wages. How many months or years a worker is ready to work for a company? Do some add-ons from time to time result in the wage to be over the wanted threshold? The pool could be, in this scenario, an open vacancies at other companies, and the probability  $p$  would be an estimate to land the position. Another case could involve a penalty for going into the pool. The idea here is to test if the penalty affects the role of quitting. How often a player quits when the punishment is low or non-existing compared to when it is high? How much is the possible gain for the individual if the penalty exists at the same time? At least, in human behavior, the fear of loss dominates more than the possibility to gain. (Professor Daniel Kahneman has done multiple psychological tests and studies about this phenomena.)

The model can be studied even further. Could the game rule be the following: quit after you face an opponent with a Hawk-strategy, be generalized up to  $K \in \mathbb{Z}_+$  match-ups? If yes, how it will affect the equilibria, and does pure-strategies become more favorable than mixed strategies or vice versa. What happens to the invasion fitness and conditions for evolutionarily stable and convergence stable strategy? Do the dynamics change radically from the dynamics I showed in this thesis? The potential for more diverse dynamics, applied to this model, is out there. Another worth mentioning point is to study the behavior of the population change in the pool between rounds. At the beginning of the game, the versatility of strategies among the players in the pool is more diverse than after  $(N - a) < N$  rounds, where  $N$  represents the end of the game and  $a$  is some positive integer. I would state this reasoning by the following: At the beginning of the game, every player is paired from the whole population, which includes all the different strategies. When the rounds go on, the pool will receive those players who choose to quit, and from those players, the new pairing will happen. The result from this behavior could end up pairing players, whose strategy is prone to quitting, against each other. Are those match-ups more favorable, in a payoff-wise, compared at the beginning of the game? Could some strategies exploit the sub-population of the pool in the middle of the game?

Earlier research of this topic does barely exists at this rate, but one exceptionally motivating thesis, discussing in passing quitting has been produced. Ollikainen (2018) introduced the idea of pooled games and quitting as a strategy, and the notion of the pool in the iterated

games of Hawk-Dove-Retaliator-Bully. Each one of these strategies I have shortly introduced in chapter two. The difference between this thesis and Ollikainen's is the handling of the strategies involved in the game. Here I had the mixed strategy included in the dynamics, whereas in Ollikainen's model, he had multiple different pure-strategies with a memory battling against each other. In both models, quitting is taken into account as a possible action and part of the equations, having an impact on payoffs. The observation from both of the thesis is the following: the role of quitting effects the game dynamics in the iterated Hawk-Dove games. It changes the position of stable equilibrium within the strategy space, allowing strategies that were not viable before be competitive against the field.

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